

THE **INSECTS** *OF* **AUSTRALIA**

A textbook for students and research workers

Second Edition

VOLUME I



Division of Entomology **CSIRO** Australia

Insects are among the most diverse and durable forms of life. In Australia alone there are over 85 000 species—overwhelmingly more than all of the vertebrate species in the entire world. Insects exhibit apparently endless variety in appearance and biology and their many peculiarities are responses to millions of years of environmental challenge and change. Insects are significant and often dominant organisms in almost all terrestrial and freshwater habitats; they are of immense importance to the stability of the environment and to human welfare.

These two volumes provide a comprehensive account of Australia's distinctive and exciting insect fauna. The volumes include detailed treatments of the morphology and biology of all insect orders and up-to-date summaries for all families known to occur in Australia. Keys using structural features, over 2000 black-and-white illustrations, colour plates and electron micrographs enable the reader to place any Australian insect in its correct family. Also featured is a unique and invaluable key to orders.

While the format of the first (1970) edition of *The Insects of Australia* has been retained in these two volumes, knowledge about Australian insects has increased enormously since 1970. All chapters have been entirely rewritten and substantially expanded, and three new chapters have been included. This new edition is the work of more than 70 experts from around the world.

Jacket illustrations: *front*: *Austrosimulium bancrofti* (Taylor), biting fly (Diptera: Simuliidae) [C. Beaton]; *spine*: *Calliphara imperialis* (Fabricius), scutellerid bug (Hemiptera: Scutelleridae) [D. C. F. Rentz]; *back*: *Lyrarmorpha* sp., nymphs, tessaratomid bug (Hemiptera: Tessaratomidae) [C. D. and D. W. Frith]; *Mastigaphoides haffneri* Weidner, katydid (Orthoptera: Tettigoniidae) [D. C. F. Rentz]; *Mictis profana* (Fabricius), crusader bug (Hemiptera: Coreidae) [J. Green]; *Petasida ephippigera* White, Leichhardt's grasshopper (Orthoptera: Pyrgomorphidae) [D. C. F. Rentz]

Donat Agosti

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Zürich

**The
Insects of
Australia**

The Insects of Australia

*A textbook for students
and research workers*

SECOND EDITION

Volume I

DIVISION OF ENTOMOLOGY
COMMONWEALTH SCIENTIFIC AND
INDUSTRIAL RESEARCH ORGANISATION



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Foreword

The first important general work on the insects of this continent, *Australian Insects* by W. W. Froggatt, was published in 1907. It was written primarily from the point of view of the field naturalist, and there is no doubt that it proved most useful to the student of those days. Nineteen years later, the classical *Insects of Australia and New Zealand* by R. J. Tillyard appeared, marking a major advance both in the content of accumulated knowledge and in the wealth of biology and comparative morphology that it presented.

'Tillyard' had long been out of print when, in 1970, the first edition of the present book was published. It was a co-operative venture, sponsored by the Division of Entomology, written largely by Divisional staff, and edited by Dr I. M. Mackerras. That the book received international acclaim was due in no small part to Mackerras's scholarship and commitment. The book has since found wide use as a student text and as an essential tool for professional entomologists.

By 1984 it was clear that the first edition (and material included in the 1974 *Supplement*) was in many respects outdated, and a revised edition was mooted. Where possible, the authors of chapters were invited to revise their 1970 texts or to recommend specialists to assist or replace them in this task. Again CSIRO entomologists assumed a major role. Specialists in other Australian and overseas institutions agreed to contribute and the book is all the more authoritative for their efforts.

The result of the revision is almost a new book. Some text and many illustrations have been retained unaltered from the first edition. However, most chapters have been rewritten entirely to incorporate the wealth of new information now available. Many new illustrations have been added, some illustrations from the first edition have been amended, and most of the plates have been rearranged and relabelled. Material of a physiological and cytological nature, or dealing with aspects of reproduction and metamorphosis, has either been incorporated into other chapters (especially an expanded Chapter 2) or omitted. In its place new chapters deal specifically with the impingement of insects on human history and economy, with the use of insects in scientific research, and with the history of Australian entomology. Another new feature is a key to the insect orders in Chapter 1.

The task of the authors/revisers of chapters was to give an account of the insects of Australia primarily from the systematic point of view, but with some account of their morphology, where they live, and what they do. To achieve even this limited objective in two volumes of reasonable size has involved rigorous selection of subject matter and imposed severe limitations on its presentation. We expect that, in consequence, few authors of the systematic chapters are really satisfied with the adequacy with which the allocated space has permitted them to cover their orders. Apart from considerations of space it has been necessary for all authors to conform rather closely to an established pattern; this they have accepted for the most part cheerfully, although they would sometimes have preferred to deviate to suit their own particular needs.

The expansion in our knowledge of Australian insects since 1926 is reflected in the increase in the number of known species and families. Tillyard estimated 37 300 species and listed 401 families. The first edition of *The Insects of*

Australia recorded 54 071 species (an increase of 45% over Tillyard) and 574 families. In the present two volumes we see the figures escalate to 85 920 (an increase of 59% over the first edition) in 661 families. These numbers reflect increased specialist exploration of the continent but alone do not depict the magnitude of the work still to be done. At least some entomologists estimate that more than half of Australia's insect species have yet to be named. The proportion of species recognisable from the literature, and for which we have even rudimentary biological and distributional data, is certainly smaller. The increases in the number of families of insects known from Australia emphasise that this continent remains an entomological frontier. Some of the new families have come from the subdivision of existing families and others result from the discovery in Australia of existing families previously not known to occur here. There have also been a few notable discoveries of entirely new, exclusively Australian families.

In the teaching of Zoology the trend for some years has been away from a taxonomic approach as a major foundation on which to build other studies. Although this may mean that books like our volumes will progressively occupy a less and less central position in the formal training of students, they will continue to be invaluable sources of information and to provide an entry into the relevant but widely scattered literature. Indeed it is not too much to hope that a work of this sort will stimulate interest in a more broadly based taxonomy than has been general in Australia in the past. The keys—many of which are new—the abundance of illustrations, and the wealth of previously unpublished biological information certainly provide the student with a broad, firm foundation to the subject.

Canberra
January 1990

D. F. Waterhouse,
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Acknowledgments

The indebtedness of individual authors to those who helped them in their work is acknowledged separately in the appropriate chapters. Here we wish to record our appreciation and thanks to those who contributed in more general ways.

The illustrations are as important as the text in a work of this kind. Most of those in these volumes are original and were made, under the guidance of the authors or editors, by the artists whose names appear in square brackets in the legends. We owe a special debt to Frank Nanninga, who painted the coloured plates and drew a great many of the line illustrations. Anne Hastings, Se Kim, Terry Nolan and Sandy Smith contributed most of the new line illustrations included in this edition. Ms Hastings, Mr Kim, Mrs Smith, Chris Hunt and Andrew Carter were responsible for the layout of illustrations and for preparation of these for the Press. John Green and Alan Edward provided the photographic prints and Colin Beaton and Helen Geier the plates of electron micrographs. Where illustrations have been redrawn from published work, this is acknowledged in the appropriate legends. We thank the Elsevier Publishing Company, Amsterdam, for permission to make direct use of Fig. 3.15 (from Berg 1975), Kluwer Academic Publishers, Dordrecht, for Fig. 35.40 (from Lawrence 1985a), and the Editors of the *Memoirs of the Queensland Museum* for Fig. 24.7 (from Rentz 1980). Several other illustrations are reproduced with the permission of the Editors of *The Australian Journal of Zoology* and *Invertebrate Taxonomy*.

Preparation of such a large manuscript in good order is an arduous business, and we are indebted to Irma Pumpurs, on whom the greatest burden fell, for the care and accuracy with which she completed her work. Eric Zurcher processed the many text files into final format for the Press. Judith Olditch, Judith Hull, Heather Baker, Patsy Gillison, Eva Bugledich and Jonathan McCabe also assisted in the keying and correcting of text. Anne Frodsham and Patricia Wellisch (Press liaison) and Ray McInnes provided invaluable support to the Editorial Committee.

The bibliography was checked by Josephine Cardale. Almost all references were confirmed against original publications and we are grateful for the help in this sometimes difficult task which we received from the staff of the CSIRO Library, Black Mountain, Canberra. Ms Cardale also compiled the index.

Many referees and some of the staff and students of the Department of Entomology, University of Queensland, commented on chapters and tested some keys. We thank them for their unselfish, anonymous contributions.

The Utah Foundation, the Ian Potter Foundation, Wellcome Australia and the University of Melbourne generously provided funds to enable the production of many new illustrations. We thank them for their continuing interest in the production of these volumes.

Finally the Editorial Committee would like to record with particular appreciation the cordial and understanding relationship that has existed between them and the Directors and the staff of the Press over what has proved to be quite a long period. Sally Paxton and Kevin Jeans of CSIRO Editorial Services and Susan Keogh, among others of the Press, were responsible for typesetting and page layout.

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(painted by F. Nanninga)

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Introduction

Insects are among the most abundant and successful of terrestrial animals. They include about three-fourths of all the described species of animals, and they have become adapted to a great range of environments, from high latitudes to the equator, from rainforest to desert, from mountains to the shore, and to varied ways of living—phytophagous, carnivorous, saprophagous, parasitic. Many have become aquatic during part or the whole of their life history. The breadth of their adaptive radiations has brought some of them, though only a very small proportion of the total, into close contact with human populations. On the one hand, they damage or destroy crops and domestic animals, transmit diseases of plants and animals, including people, and damage or destroy human habitations. On the other hand, humans have added bees and silkworms to their flocks, and have learned to use other species to control noxious insects and weeds. Moreover, insects have provided some of the most valuable tools of biological research in many fields from the broadest aspects of evolution to the detailed mechanisms of inheritance.

It is natural, then, that entomology should have shared in the steadily increasing volume of research that has made it so difficult to be both brief and comprehensive when reviewing any scientific discipline. Selection is unavoidable, and the purpose of these notes is to set out the scope of this book and the ways in which problems of presentation and compression have been met.

1. It has been necessary to assume that the reader would have a background of general knowledge equivalent to what might reasonably be expected at the end of the first year of a university course in Science. This may

impose some hardship on the amateur entomologists who may wish to use the book, but it is hoped that they will find sufficient explanation in the text and illustrations to meet their needs. There is no glossary. Terms with which the reader might not be familiar are defined in the text and entered in the index.

2. Chapters 1 to 10 have been reduced to the minimum that is considered essential for the general student of entomology as a background for the chapters that follow. Chapter 1 has presented particular difficulty in this respect, because the anatomical terminology used in it has been based, as far as possible, on usage among morphologists, whereas the writers on many of the orders carry the historical burden of a terminology that has grown up with little or no reference to what has been done outside those orders. There seems to be no way to avoid this unfortunate situation. There is the further minor difficulty that the earlier chapters must anticipate Chapters 5 and 6, but a general picture of the classification used may be obtained by referring to Figs 5.1 and 5.5. Chapter 6 differs from other chapters in a few interpretations of morphology.

3. The presentation of the remaining chapters is essentially systematic, an arrangement that serves to emphasise the evolutionary perspective into which any study of insects should be fitted. The systematic statements have been used as pegs on which to hang short accounts of where the insects live and what they do. Wider problems are touched on when describing insects that illustrate them particularly well.

4. The book is designed to cover Australian insects only. The insects of New Zealand, New Guinea and the

Pacific are referred to here only when they are relevant to particular problems that are being discussed. However, an attempt has been made to put the Australian fauna into perspective with that of the rest of the world by including at least a mention of important groups that do not occur here. There are abbreviated chapters dealing with the small orders not represented in Australia.

5. In the systematic chapters the censuses include undescribed species and unrecorded synonymy known to the authors, but the completeness of this information differs from order to order, so the figures should be taken as approximations. Their reliability as indices of the total number of species in the country varies greatly. Thus, it is reasonable to suppose that most of the species of Australian butterflies and mosquitoes are already known; the same cannot be written of the less-studied families of Lepidoptera and Diptera.

6. The keys to families and higher taxa have been based primarily, though not exclusively, on Australian material. Some of them may have a wider application, but they should be used with reserve for placing specimens from other regions. There has not been room for more than a few keys below the family level.

7. Common names have been used sparingly, and only for widely known species. A full list, with standard abbreviations of the names of authors of species, is given by Carne (1987). The techniques of collecting, preserving, and studying insects have been described by Upton (1991).

8. The following abbreviations have been used, where appropriate, for political divisions of Australia:

Qld	Queensland;
N.S.W.	New South Wales;
Vic.	Victoria;
S.A.	South Australia;
W.A.	Western Australia;
N.T.	Northern Territory;
A.C.T.	Australian Capital Territory.
Tas.	Tasmania

T1 denotes the first abdominal tergum (or tergite), T2 the second, etc.; S1, S2, etc. denote the corresponding abdominal sternite (or sternites).

Where appropriate, ordinal names are abbreviated as follows:

COLL	Collembola;
PROT	Protura;

DIPL	Diplura;
ARCH	Archaeognatha;
THNU	Thysanura;
EPHM	Ephemeroptera;
ODON	Odonata;
PLEC	Plecoptera;
BLAT	Blattodea;
ISOP	Isoptera;
MANT	Mantodea;
GRYL	Grylloblattodea;
DERM	Dermaptera;
ORTH	Orthoptera;
PHAS	Phasmatodea;
EMBI	Embioptera;
ZORA	Zoraptera;
PSOC	Psocoptera;
PHTH	Phthiraptera;
HEMI	Hemiptera;
THPT	Thysanoptera;
MEGA	Megaloptera;
RAPH	Raphidioptera;
NEUR	Neuroptera;
COLE	Coleoptera;
STRP	Strepsiptera;
MECO	Mecoptera;
SIPH	Siphonaptera;
DIPT	Diptera;
TRIC	Trichoptera;
LEPI	Lepidoptera;
HYMN	Hymenoptera.

9. References have presented a particular problem. It is impossible to give extensive bibliographies in the space available, and reliance has been placed as much as possible on references to reviews and monographic works which provide a recent, readily available entry into the major literature. It must be stressed that this in no way implies any lack of appreciation of earlier classical papers. Direct study of these works is indispensable to any serious student, and some of them have been referred to in general terms when the full references are included in a publication that is cited. References in round brackets relate to the statements in which they occur, those in square brackets usually to the group as a whole. Papers on Australian insects up to 1930 have been listed in the bibliography by Musgrave (1932).

Skeletal Anatomy and Key to Orders

J. F. LAWRENCE, E. S. NIELSEN *and* I. M. MACKERRAS

Arthropods are metamerically segmented invertebrates with articulated exoskeletons, which not only provide support for soft tissues, attachments for muscles, and protection from physical stresses, but determine the external appearance of the animals as well. Consequently, this chapter is concerned primarily with the external anatomy of the adult insect. It includes the infoldings and appendages, but does not take the detailed structure of the cuticle into account, and it is intended to provide no more than a background for later chapters. Fuller descriptions, with references to literature, will be found in Snodgrass (1935, 1952), Richards and Davies (1977), Matsuda (1965, 1970, 1976, 1979), Bitsch (1979) and Denis and Bitsch (1973); von K  ler (1955) and Nichols (1989) provide useful glossaries of morphological terms.

A major difficulty facing the student is the plethora of anatomical terminologies that are used in the different orders. To some extent this is inevitable, because the comparative anatomy and embryology of some groups have not been studied in sufficient detail for firm conclusions to be drawn. This kind of difficulty is well illustrated by the external genitalia (Tuxen 1970b). When these legitimate reasons for disparities have been taken into account, there remain a still greater number that are due to the fact that specialists on different orders have developed their own terminologies without reference to homologies.

ORIENTATION AND RELATIONSHIP OF PARTS

It is necessary to define some general terms at the outset. An insect is, basically, a bilaterally symmetrical, horizontally oriented, forwardly progressing animal, and its body can consequently be divided by three sets of primary anatomical planes at right angles to each other (Fig. 1.1): vertical *sagittal* planes in the direction of its long axis, the one passing through the central axis of the body being the *median sagittal plane* or *meson*; horizontal planes, also parallel with the long axis; and *transverse* planes at right angles to its long axis and to the other two planes. The head end of the body is *anterior*, *cranial* or *cephalic*, the hind end is *posterior* or *caudal*, and the anteroposterior relationships of parts are described by these adjectives. The upper surface is *dorsal* and the lower surface *ventral*. Structures lying nearer to the median sagittal plane than other structures are referred to as being *mesal* (or *medial*) to them; those lying further from this plane or closer to

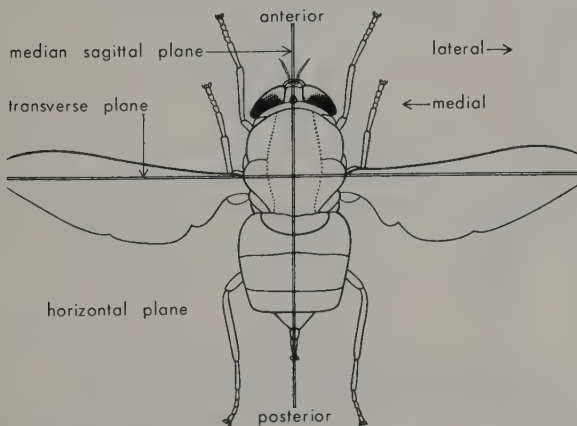


Fig. 1.1 A generalised fly (*Pelecorhynchus fusconiger*, ♀) showing orientation and anatomical planes. [B. Rankin]

the sides of the body than others are *lateral* to them. The term *sublateral* is sometimes used for structures or areas lying near the outer edges of the body. Similarly, parts of appendages (or of other attached structures) that lie nearer to the body are referred to as *proximal* or *basal* and those further from the body as *distal* or *apical*. Combined terms, such as dorsolateral, anteroventral or apicolateral, may also be used. The suffix '-al' is sometimes replaced by '-ad' to denote direction; thus mesad means towards the middle and a structure may be 'mesad of' another structure.

All these terms are used in relation to the morphologically horizontal position of the insect, no matter what attitude it may take up; thus, care in interpretation is necessary, particularly in defining the surfaces of leg segments. It cannot be stressed too much that precise terms should always be used to describe anatomical relationships.

GENERAL ORGANISATION

Insects are composed of about twenty original somites. They show considerable advance on their presumed myriapodan ancestors in having developed a much greater degree of *tagmosis*, which is the co-ordination or amalgamation of segments to perform some particular group of functions. As Tiegs and Manton (1958) have stressed, tagmosis has been vitally important in the evolution of

insects, because, originally developed in response to some immediate need, each episode of tagmosis has opened the way for further adaptive radiation. The result has been the division of the insect body into the three familiar regions of *head*, *thorax* and *abdomen*, each with its specially modified appendages (Fig. 1.2).

The head consists of (1) the *procephalon*, which bears the eyes, antennae and labrum, and (2) the *gnathocephalon*, three postoral appendage-bearing segments fused to the procephalon to provide mouth-parts. The composition of the procephalon is somewhat debatable, but generally it is subdivided into *protocephalon* (ocular region), *deutocephalon* (antennal region) and *tritocephalon* (clypeo-labral and premandibular regions), based on their innervation from the protocerebrum, deutocerebrum and tritocerebrum, respectively (see p. 43). The gnathocephalon is subdivided into mandibular, maxillary and labial segments, which are innervated by portions of the suboesophageal ganglion. The thorax consists of three somites, which are still more or less clearly distinguishable as separate segments. Originally developed in response to the adoption of a hexapod gait, it provided the point of balance at which wings could function effectively, and became further enlarged and modified when they evolved on its second and third segments. The abdomen remained relatively unmodified, except that the appendages of most of its segments atrophied, although they

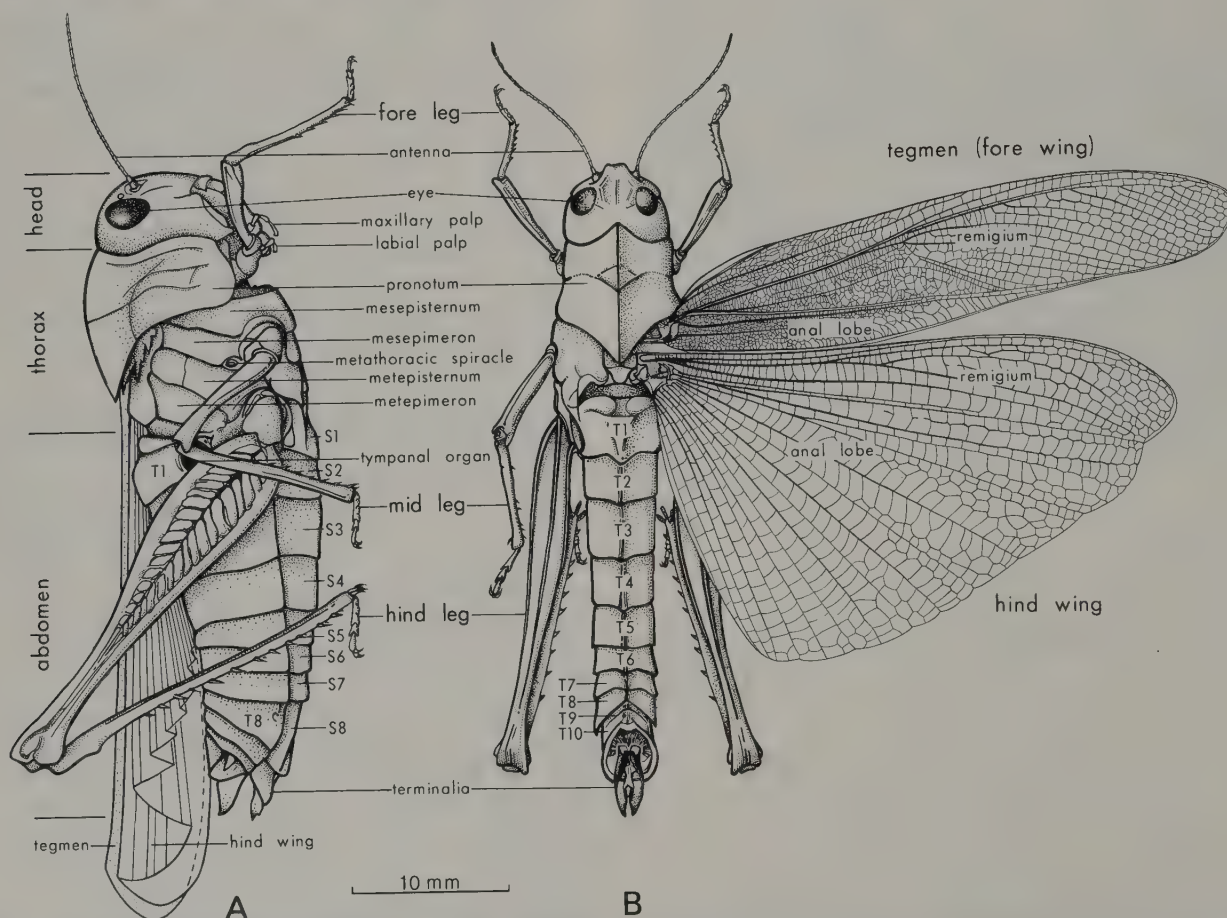


Fig. 1.2 A common locust (*Gastrimargus musicus* (ORTH), ♀) showing main anatomical divisions and landmarks.

[T. Nolan]

can still be seen in the apterygotes and the embryos of higher insects. It consisted originally of 11 segments, and there is a minor degree of tagmosis in the terminal segments.

The primitive metameric segmentation is indicated in unsclerotised larvae by the insertions of the longitudinal segmental muscles and by corresponding transverse segmental grooves on the surface of the body (Fig. 1.3A). When sclerotisation develops, it does so in dorsal and ventral plates extending from just anterior to each intersegmental groove (*antecostal suture*) for a varying distance towards the posterior end of the segment. The inflected part is the *antecosta*; the strip anterior to it is the *acrotergite* dorsally and the *acrostermite* ventrally; and the posterior part of the plate is the body of the *tergum* dorsally and of the *sternum* ventrally (Fig. 1.3B).^{*} The unsclerotised part of the segmental cuticle posterior to the tergal and sternal plates is the so-called *conjunctival* or *intersegmental* membrane, which generally becomes tucked in as the plates extend (Fig. 1.3C).

In this way, a secondary functional segmentation is imposed on the primary metameric segmentation. In the abdomen the sides (*pleura*) of the body remain membranous; but in the thorax, where greater rigidity is required, strengthening sclerites are laid down in the pleural membrane, and become associated with the tergal and sternal plates to form a box with a precisely limited capacity for distortion. In the head, where no flexibility at all is needed, all the sclerites become fused into a single strong

capsule. In addition, there are sclerotised infoldings (*apodemes*) projecting into the body to add strength and provide muscle attachments; these apodemes may be called *endotergites*, *endopleurites* or *endosternites*, according to location or origin, and are sometimes referred to as *apophyses*, *furcae*, *phragmata* or *spinae*, based mainly on shape.

Finally, the appendages (e.g. legs, wings, terminalia) consist mainly of segmented or non-segmented tubes or plates with flexible articulations at the joints, and the air-filled tubes (*tracheae*) of the respiratory apparatus open at segmental *spiracles* on each side. Various parts of the body may also be more or less covered with hairs of different kinds—*macrotrichia*, which may be modified into spines or scales, and *microtrichia*, which may become specialised into the fine pile of a plastron. The arrangement of the hairs (*chaetotaxy*) is often of taxonomic value.

HEAD

Cranium

The skull of an insect (Fig. 1.4) is a hard, usually more or less globular capsule, which is incomplete below (where the preoral cavity is partly closed by the mouth-parts), and opens posteriorly by the *occipital foramen* (Fig. 1.5), through which the nerve cords, oesophagus, aorta, salivary ducts, and a pair of tracheae enter or leave the neck. The part dorsal and anterior to the occipital foramen is the *epicranium*, which is divided into the *occiput* posteriorly, the *vertex* dorsally, the *frontoclypeus* anteriorly, and the *genae* (cheeks) laterally, although the limits of these areas are often not clearly defined.

The inflected skeleton or *tentorium* is formed by pairs of apodemes, the most important of which are the *anteri-*

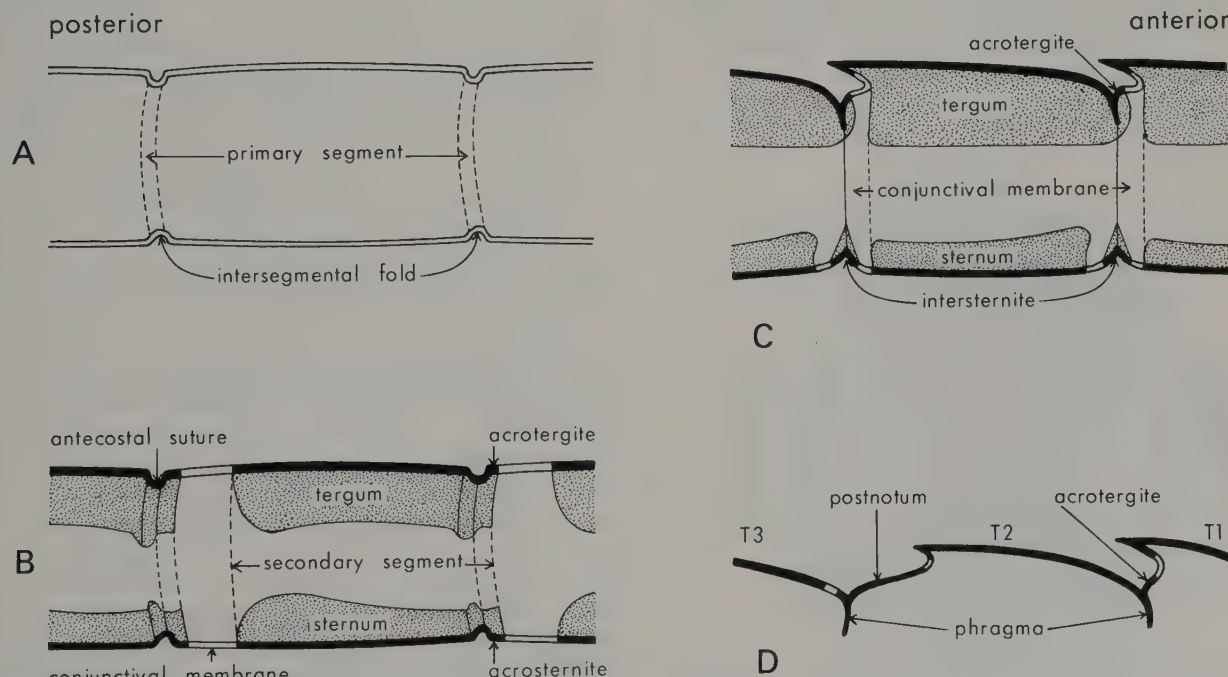


Fig. 1.3 Diagrams of primary and secondary segmentation (based on Snodgrass 1935): A, primary; B, simple secondary; C, more advanced secondary; D, dorsal sclerites of thorax in section.

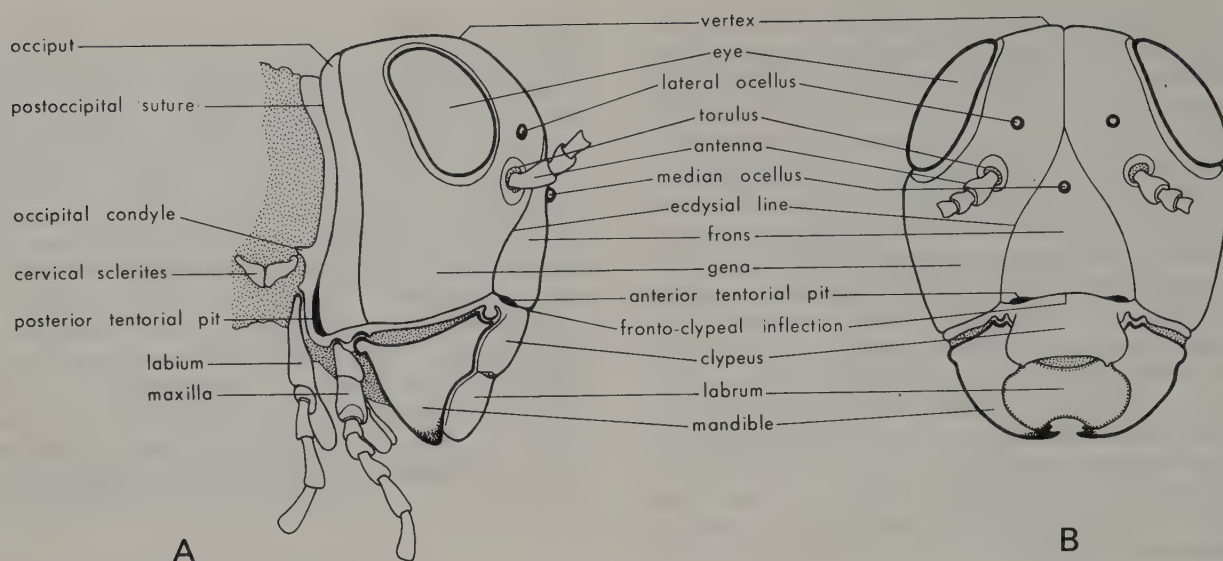


Fig. 1.4 A generalised cranium: A, lateral; B, anterior.

[After Snodgrass 1935]

or tentorial arms (*pretentorium*) and the *posterior tentorial arms* (*metatentorium*); each of the anterior arms may also bear a *dorsal tentorial arm*. Posterior tentorial arms are absent in entognathous hexapods, and in the Pterygota the posterior and anterior arms are fused. The right and left sides of the tentorium may bear mesal, plate-like projections, called *laminatentoria* and may be joined by a bridge known as the *corpotentorium*. In the Dictyoptera (Blattodea, Isoptera, Mantodea) the arms are united to form a *frontal plate* anteriorly and a *corpus tentorii* posteriorly, with a more or less extensive gap or foramen between them (Fig. 1.5). Other internal ridges occur less consistently, for example between frons and clypeus, between both of these and the genae, around the eyes, or around the antennae. All may show indications of their presence in the form of external grooves or 'sutures', and thus provide useful anatomical landmarks.

Compound eyes are present in most adult insects. They usually occupy a considerable area on each side of the

head. When so large that they meet in the median line, they are termed *holoptic*; when separated, they are *dichoptic*. Externally, the eye consists of a large number of hexagonal *facets* (or corneal lenses) formed of transparent cuticle, each lens representing the outer portion of a single eye element or *ommatidium*. Sometimes the upper facets are much larger than the lower, and occasionally the eyes are divided into separated dorsal and ventral parts. They may show a pattern of bands or patches of contrasting colour in life, and the interfacetal junctions are often provided with fine hairs, which may be dense enough to give the eyes a distinctive appearance.

Three *ocelli*, typically arranged in an isosceles triangle on the vertex, are present in so many insects that they are presumed to have occurred in the common ancestor. Each *lateral* (or posterior) ocellus has a single lens, but differs from an ommatidium of a compound eye in that the lens covers a number of internal eye elements. The *median* (or anterior) ocellus was apparently formed from two separate ocelli which became fused together, and it is innervated from both sides of the deutocerebrum.

With the main areas and landmarks of the cranium thus broadly defined, we may turn to the problems presented by the so-called sutures of the head (see DuPorte 1957; Hinton 1958c).

In the first place, the only lines that may represent original segmental divisions of the cranium are the *postoccipital suture* just anterior to the occipital foramen in many insects (Fig. 1.4A), and a suture anterior to this in Archaeognatha, which may mark off the maxillary segment (Snodgrass 1935). Other significant lines are the epicranial and fronto-clypeal sutures (see below).

Secondly, there are two kinds of 'sutures'. The first is represented by the dorsal and ventral *ecdysial lines*, along which the capsule splits or hinges in immature insects, and which persist as unpigmented lines in some adults. The dorsal lines, collectively known as the *epicranial suture*, typically form an inverted Y, with the median *coronal arm* extending forward from the occiput and the

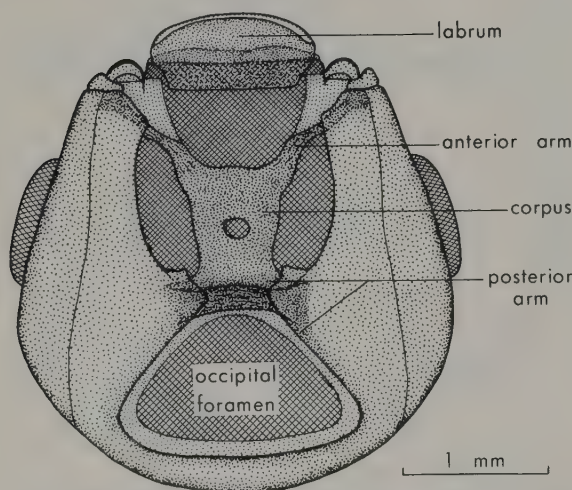


Fig. 1.5 Tentorial skeleton of *Mastotermes darwiniensis* (ISOP), ♂.

two lateral, or *frontal*, arms diverging between the ocelli (Fig. 1.4B). The ventral lines may be single or double, and they may enclose a median area, the *ventral apotome*, the position and extent of which is of functional rather than morphological significance (Hinton 1963b). All these lines vary in position, and they may become incorporated in, or confused with, other depressions.

The second kind of suture is formed by inflections of the surface which are normally associated with apodemes. They are generally better defined than the ecdysial lines, but their positions are also determined primarily by functional requirements, and they do not necessarily mark off morphologically identical areas in different insects. The most constant and conspicuous inflections are the *anterior tentorial pits* (*pretentorinae*), which mark the origins of the anterior tentorial arms. There is a less conspicuous pair of *posterior tentorial pits* (*metatentorinae*) marking the origin of the posterior tentorial arms on either side of the occiput, and these may lie on an inflection dividing the occiput from the posterior genae behind the eyes. Anteriorly, the *fronto-clypeal* or *epistomal* inflection or 'suture' joins the tentorial pits, and it may separate the *frons* above from the *clypeus* below. Laterally the frons may be separated from the genae on each side by a deep *fronto-genal* inflection, which is continued below the tentorial pits as a *clypeo-genal* inflection.

While the frons may be regarded, basically, as extending from the vertex to the fronto-clypeal inflection or, in its absence, to a horizontal line joining the anterior tentorial pits, the landmarks are not always clear, and there may be additional inflections on the frontal or clypeal areas. Consequently, some systematists adopt purely topographical definitions, limiting the frons to the area dorsal to the insertions of the antennae, and calling the whole or part of the central area bounded by the antennal insertions dorsally, the labrum ventrally, and the fronto-genal and clypeo-genal inflections laterally, the *face*.

When a median ventral sclerite is differentiated behind the labium, especially in prognathous insects, it is termed the *gula*, or gular plate, when behind/above the posterior tentorial pits, and termed a hypostomal bridge when in front of/below the tentorial pits.

Antennae

These are a pair of mobile, segmented appendages, which are inserted in the head between the eyes. The articulation to the skull often consists of a sclerotised ring forming a socket (*torulus*), and there may be a projecting peg, rarely two, which provides for free movement of the antenna in all directions. Three principal divisions of the antenna may usually be recognised (Fig. 1.6): the *scape*, or basal

segment, often longer or larger than any of the succeeding segments, and containing the intrinsic muscles; the *pedicel*, or second segment, which is filled with a mass of scolopophorous sensilla called Johnston's organ (see p. 44) and the *flagellum*, which forms the remainder of the antenna and is usually multisegmented. Individual antennal segments are sometimes referred to as *antennomeres*, and those comprising the flagellum may be called *flagellomeres*. Antennae are of many diverse forms, which are described under the various orders. Functionally, they are organs of chemoreception, thermoreception and hygroreception, and are provided with a variety of sensory pegs and setae. Antennae often display obvious secondary sexual characters. Those of the male may be greatly enlarged or modified to increase the surface area (and thus the ability to detect pheromones produced by the female), or in some cases antennal modifications may be involved in courtship behaviour.

Mouth-parts

The *preoral cavity*, which opens posteriorly into the definitive mouth, is bounded anteriorly by the labrum, posteriorly by the labium, and laterally by the lower margins of the genae; the mandibles and first maxillae are articulated at its sides (Fig. 1.7). The former is attached to an area known as the *pleurostoma*, the latter to a contiguous area known as the *hypostoma*. In contrast with those of other hexapods the mouth-parts of true insects are primitively exposed (*ectognathous*) and ventrally projecting (*hypognathous*) (Fig. 1.4A). In various groups, however, the orientation of the head has changed, so that the mouth-parts are *prognathous* (i.e. projecting anteriorly, Fig. 35.3A) or *opisthognathous* (i.e. projecting posteriorly, Figs 30.1, 2, 16, 18). There are many variations in detail, depending on the method of feeding, and the following general description is based on an insect with mouth-parts adapted for biting and chewing (Figs 1.4, 7).

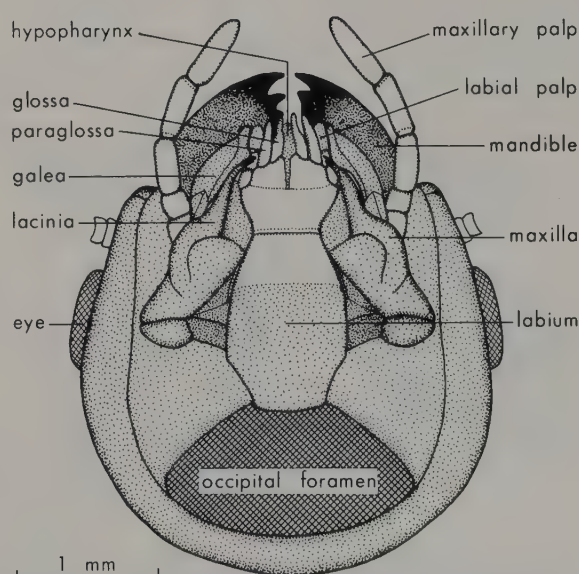


Fig. 1.7 Head of *Mastotermes darwiniensis* (ISOP), ♂, posteroventral, showing relationships of mouth-parts. [B. Rankin]

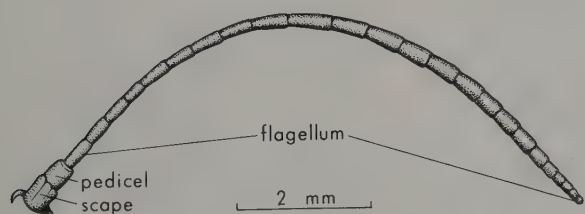


Fig. 1.6 Antenna of *Gastrimargus musicus* (ORTH), ♂. [B. Rankin]

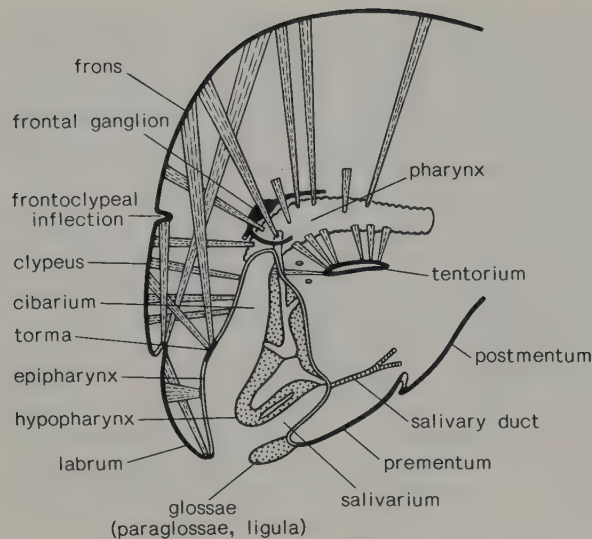


Fig. 1.8 Head of a generalised insect (parasagittal section) showing musculature associated with the cibarium and pharynx.
[After Denis and Bitsch 1973; S. P. Kim]

The *labrum* is normally a movable plate attached to the lower margin of the clypeus (Figs 1.4, 8). Its outer surface is generally strongly sclerotised, and its distal margin sharply defined; its internal surface, the *epipharynx*, is membranous and furnished with small tactile hairs and taste organs. A pair of small sclerites, the *tormae*, may be present at the basolateral angles of the labrum.

The *mandibles* (Fig. 1.9A) are a pair of strongly sclerotised, usually toothed jaws situated immediately posterior to the labrum. Except in Archaeognatha, they primitively articulate with a process of the clypeus anteriorly by a ginglymus (hinge) joint and with the gena posteriorly by a condyle (ball), and they are operated by what are usually the most powerful muscles in the head. They are the principal feeding organs, being used primitively to bite off and chew the food. They are not segmented (apparent segmentation in some fly larvae is undoubtedly secondary) and they do not have a palp. An accessory *prosthema* ('*lacinia mobilis*') occurs in the Diplura and is scattered among pterygote insects as well.

The *maxillae* (first maxillae) (Fig. 1.9B) lie posteroventral to the mandibles and anterodorsal to the labium. They differ from the mandibles in showing evidence of having originated by modification of walking legs, and they are usually divided into several parts. The first segment is the *cardo*, which is attached to the head proximally and to a longer second segment, the *stipes*, distally. The stipes bears two lobes, the lateral *galea* and the mesal *lacinia*. The maxillary *palp*, or *palpus*, usually of one to seven segments, is attached laterally to the distal part of the stipes, sometimes by a separated section, the *palpifer*. There is considerable variation, the galea sometimes being two-segmented and the lacinia spined or toothed on its mesal border. The maxillae serve as accessory jaws, the laciniae helping to hold the food when the mandibles are extended, as well as assisting in mastication, and the galea and palp assisting to select the food by touch and taste.

The *labium* (Fig. 1.9C) consists of the fused second maxillae. It is attached to the ventral surface of the cranium (to the gular plate, if that sclerite is developed), is bilaterally symmetrical, and is divided into the following parts: *postmentum* proximally; *prementum* more distally; two distal processes articulated to the prementum on each side, the *glossa* mesally and *paraglossa* laterally; and a pair of labial palps, normally of one to four segments, arising from a lateral part of the prementum which is sometimes differentiated as the *palpiger*. When the prementum is divided transversely into two parts, the distal portion bearing the glossae and paraglossae is known as the *ligula*.

In addition to the paired mouth-parts, there is primitively a median, unpaired, tongue-like organ, the *hypopharynx*, projecting forward from the back of the preoral cavity, and dividing it into a dorsal *cibarium*, which serves as a food-pouch, and a ventral *salivarium*, into which the salivary ducts open (Fig. 1.8). The primitive hypopharynx has an elaborate complement of sclerites and it bears a pair of lateral lobes called *superlinguae* (lost in the vast majority of hexapods). Among pterygote insects only mayfly nymphs have retained unequivocal superlinguae; paired basal or apical lobes on the hypo-

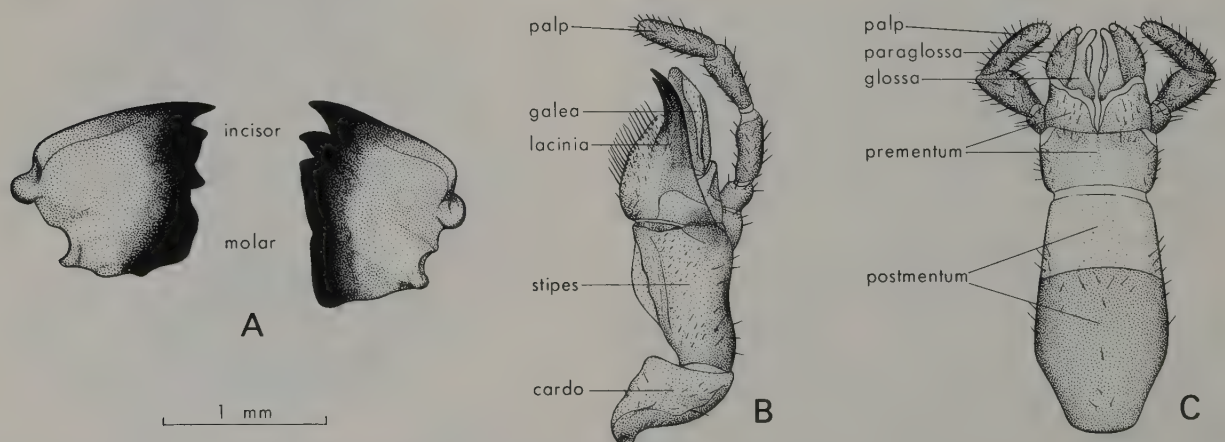


Fig. 1.9 Mouth-parts of *Mastotermes darwiniensis* (ISOP), ♂: A, mandibles; B, right maxilla; C, labium.

[B. Rankin]

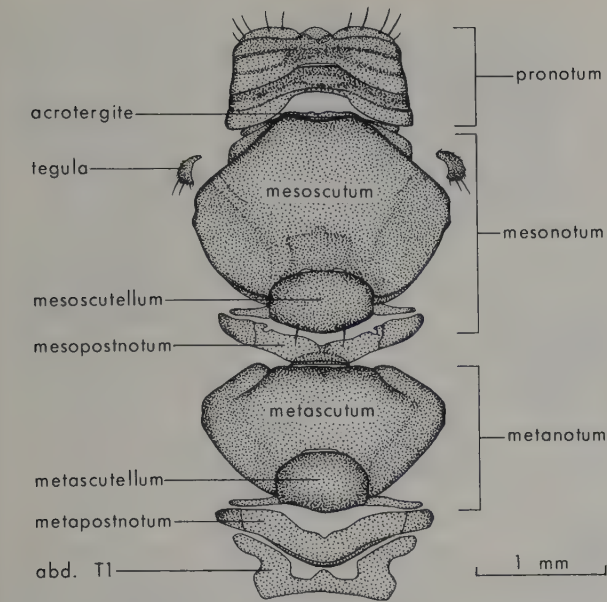


Fig. 1.10 Dorsal thoracic sclerites of *Chorista australis* (MECO), ♀. The prescuta are not clearly defined.

pharynx in other pterygotes are probably secondary formations (Denis and Bitsch 1973).

There are a great many variations in this basic pattern. In lucanid beetles there is marked sexual dimorphism in the size and shape of the mandibles. In sucking insects both mandibles and maxillae may be transformed into spear-like organs (*stylets*), or the mandibles may disappear; the maxillary stylet may be derived from the lacinia, or the galea, the other parts being reduced or absent; in the vast majority of the Lepidoptera (Figs 41.1, 22) the laciniae disappear and the two galeae together form the haustellum or coiled sucking tube. The labium may be drawn out into an elongate, sometimes segmented trough to hold the other mouth-parts, and its palps may be absent (Hemiptera) or reduced to a pair of lobes (*labella*) at its distal end (Diptera). The hypopharynx is sometimes complexly fused with parts of the labium, and in the Diptera the composite formation is stylet-like, bearing the salivary orifice apically.

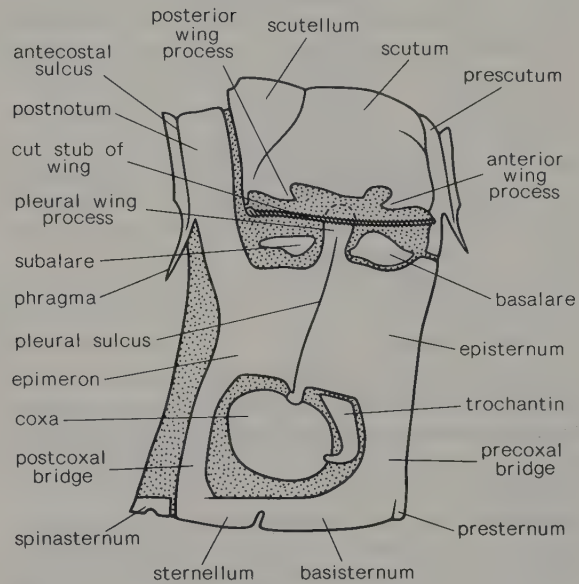
THORAX

The head is joined to the prothoracic sclerites by a flexible, membranous neck of mainly prothoracic origin; the neck is usually quite short, and generally strengthened by small sclerites to which the muscles that control the movements of the head are attached.

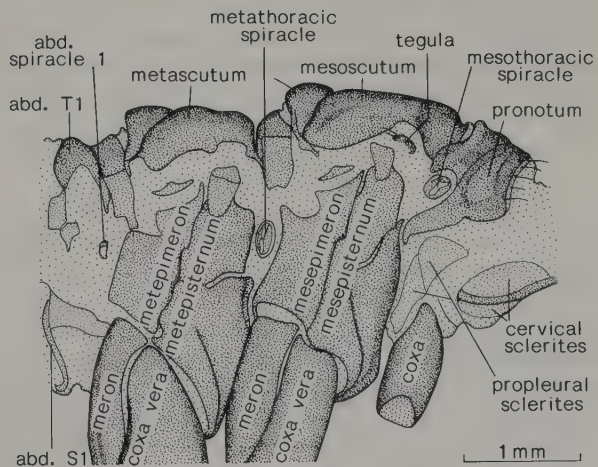
The segments of the thorax are the *prothorax*, *mesothorax* and *metathorax* (Figs 1.10, 11), and their sclerites carry the same prefixes, for example, pronotum, mesepimeron; these are not to be confused with the prefixes pre- and post- which are used to define particular parts of each segment. Primitively, the three segments are similar to each other, but in the winged insects the mesothorax and metathorax are enlarged and more closely united to form a relatively rigid *pterothorax*. The prothorax is sometimes reduced to a small annulus, but in some

insects, such as cockroaches, its dorsal part is developed into a shield. The mesothorax is largest in those insects in which the fore wings are the stronger, notably in the Diptera, whereas those that fly with their hind wings or have powerful hind legs generally have a large metathorax.

The conjunctival membrane is reduced, and the sclerites cover most, or sometimes all, of the thorax. Dorsally, each tergal plate is known as a *notum*, which is usually more or less clearly subdivided into *prescutum*, *scutum* and *scutellum* (Fig. 1.10). Additional rigidity is provided by the antecostae and acrotergites. When the acrotergites remain narrow and retain their association with the notum posterior to them, they also retain their name; when they develop into wider plates associated with the notum anterior to them (to which they really belong morphologically), they are called *postnota* (Fig. 1.3D). Thus the



A



B

Fig. 1.11 A, Diagrammatic lateral view of typical wing-bearing, thoracic segment. B, Thorax of *Chorista australis* (MECO), ♀, lateral view.

[A after Snodgrass 1935]

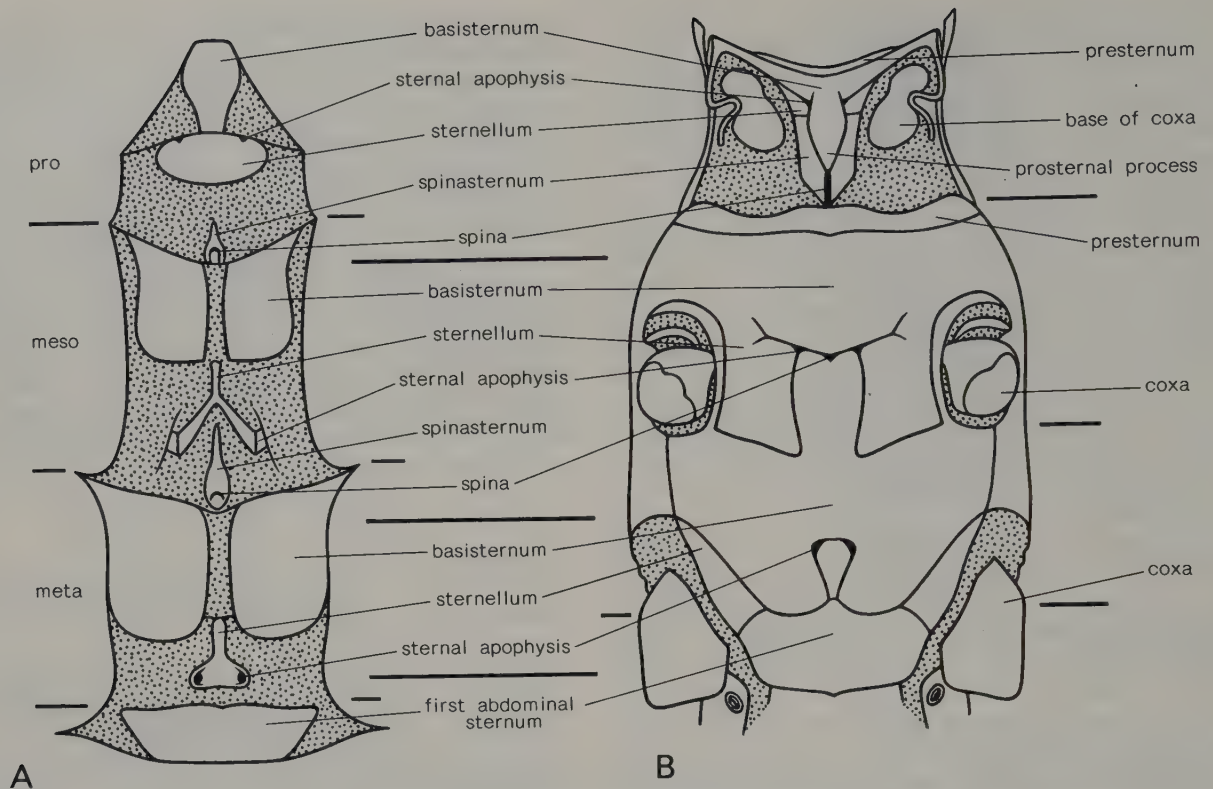


Fig. 1.12 Ventral views of the thorax: A, *Blatta orientalis* (BLAT); B, *Nomadacris septemfasciata* (ORTH).

[After Chapman 1982; S. P. Kim]

metathorax has both acrotergite and postnotum in the Orthoptera and Coleoptera. On wing-bearing segments of Neoptera, there are also three (and possibly more) lateral projections, which provide hinge-joints for the bases of the wings.

The pleural sclerites laterally (Fig. 1.11) are thought to have been derived from subcoxal elements of the ancestral legs, which became incorporated into the lateral body wall. They are relatively small and variable in the apterygotes, but more extensive in the winged insects, on each segment of which they consist of an anterior *episternum* separated by the *pleural suture* from a posterior *epimeron*; the pleural suture runs from pleural wing articulation to the pleural coxa articulation and reinforces both. There is considerable variation, and the episternum may be divided into an upper *anepisternum* and lower *katepisternum*, while similar divisions of the epimeron have been named *anepimeron* (or pteropleuron) and *katepimeron*. Sometimes the episternum (or its katepisternum) is fused below with the sternum, and the combined plate is known as the *sternopleuron*. Another variation, seen most often in primitive orders and in the mesothorax of Hymenoptera, is a separation of the anterior part of the episternum as a distinct plate, the *prepectus*. The wing-bearing segments also have a *pleural wing process* for articulation with the base of the wing, together with one or more small *basalar* sclerites anterior to the process and *subalar* sclerites posterior to it, which serve for attachment of some of the direct wing muscles. There are only two pairs of *thoracic spiracles*, mesothoracic and metathoracic, in true insects. They normally lie in or near

the upper part of the divisions between the segments and the mesothoracic spiracles often appear to be on the prothorax.

The sternal plates (*eusterna*) may be simple, or divided into three sclerites, *presternum*, *basisternum*, and *sternellum* (Fig. 1.12), and in generalised insects the basisternum is separated from the sternellum by a transverse suture connecting the apodemal pits at the origin of the furcal arms. The *spinasternum* (*post-sternellum*) follows the sternellum, and corresponds to the postnotum; it is often derived from an intersternite between the segments rather than from an acrosternite. Separate *laterosternites* are sometimes found at the sides of the eusternum, and fusion of the sternal and pleural regions may result in the formation of precoxal and postcoxal bridges. The sterna may be narrow, or largely unsclerotised; they may be marked by a median longitudinal inflection; or they may become incorporated in a sternopleuron, as in the mesothorax of many Diptera.

The principal inflected skeleton of the thorax (Fig. 1.13) consists of *phragmata* (*endotergites*), extending inwards from the antecostae dorsally; lateral apodemes (*endopleurites*), formed in the wing-bearing segments by infolding along the pleural suture, and sometimes produced into mesal arms which may fuse with the furcae ventrally; and *furcae* (*endosternites*), arising from the apodemal pits between the basisterna and sternella, and generally forming Y-shaped bodies internal to the ventral body wall. In generalised insects there is also a median *spina* projecting into the body from the spinasternum, but it is usually lost or consolidated with the furca in higher

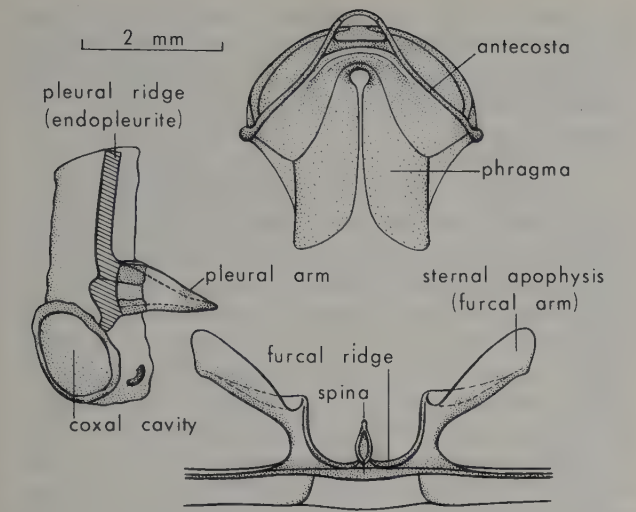


Fig. 1.13 Internal mesothoracic skeleton of *Gastrimargus musicus* (ORTH), ♂, posterior aspect, 'exploded', showing inflected phragma from tergum (endotergite), inflected ridge and apophysis from pleuron (endopleurite), and inflected spina and furca from sternum (endosternite). [B. Rankin]

forms. These apodemes provide surfaces for attachment of the large thoracic muscles.

LEGS

The insect leg (Fig. 1.14) is generally thought to consist of six segments: coxa, trochanter, femur, tibia, tarsus and pretarsus bearing the claws; the tarsus is usually subdivided into several segments, although it is still moved as a whole by a single pair of muscles arising from the distal end of the tibia. Three additional segments, occurring in many fossil insects and related arthropod groups but in very few Recent insects (e.g. some Ephemeroptera and Odonata), have been recognised: prefemur (fused with the trochanter), patella (fused with the tibia) and basitarsus (aligned with the subsegmented tarsus) (see Chapter 6). For purposes of orientation, the legs are treated as if they were extended horizontally at right angles to the body, so that the segments present dorsal, ventral, anterior and posterior aspects for examination.

The *coxa* is usually short and stout; in the pterothorax of many Neoptera it is divided into an anterior *coxa vera* and a posterior lobe, the *meron*. It articulates with the thorax by a *coxal process* at the ventral end of the pleural suture, and sometimes also with a separate plate (*trochantin*) or with the sternum, either serving to restrict its range of movement. Other articular plates occur in some insects.

The *trochanter* is usually a short segment interposed between the coxa and the femur, sometimes freely articulated with both, occasionally divided into two parts, but often firmly attached to the femur, for which it provides a coxal articulation.

The *femur* is generally the stoutest, strongest and sometimes the longest segment of the leg. It is sometimes armed with strong spines, but not with movable spurs.

The *tibia* is often longer than the femur, but nearly always more slender; it may be spiny, and is often armed with one or more articulated subapical spurs, which are occasionally very large.

The *tarsus* is usually divided into five segments (*tarso meres*) of which the first is often the longest and may be called the *basitarsus* or *metatarsus*. The number of tarsal segments varies from five down to one in different groups. The *pretarsus* (Fig. 1.14B) (also referred to as the *postitarsus*) is closely associated with the distal end of the last tarsal segment. It normally consists of two ventral sclerites, the *unguitractor plate* and the *planta*, a pair of claws, which vary in size and are sometimes toothed, and a projecting central lobe, the *arolium*. There may be a pair of pads, the *pulvilli*, between the claws, and the arolium is usually replaced by a more ventrally situated *empodium*. In some insects, *pulvilli* (*euplantulae*) occur on the ventral surface of other tarsal segments.

Normally, all three pairs of legs are used for running (and are referred to as *cursorial*) or for walking (*gressorial*); but they are employed only for perching and seizing prey in the Odonata, mainly for clinging to flowers in nectar-feeding Diptera, and are specialised for swimming (*natatorial*) in many aquatic Coleoptera and Hemiptera. The mid legs usually remain relatively simple, but the fore or hind may become extremely specialised, the fore legs for seizing prey (*raptorial*) or for digging (*fossorial*), and the hind enlarged for jumping (*saltatorial*). The mid

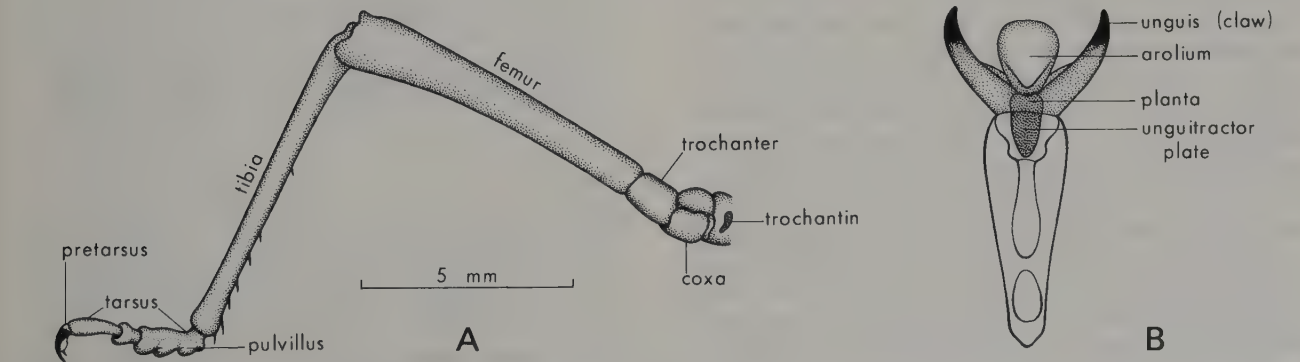


Fig. 1.14 Mid leg of *Gastrimargus musicus* (ORTH), ♂: A, anterior view; B, last tarsal segment and pretarsus, ventral. [B. Rankin]

or hind legs are raptorial in some Diptera and the hind in some Mecoptera. The fore legs of male Ephemeroptera are characteristically lengthened to hold the female in copulation, whereas the mid and hind may be more or less atrophied.

WINGS

Hypotheses concerning the origin of insect wings generally fall into two classes: those deriving wings from (1) rigid, lobe-like expansions (*paranotal lobes*) of the thoracic terga, which became secondarily articulated and muscled, or (2) pre-existing, articulated and muscled appendages (including gills and styli) located at the bases of the thoracic legs. The *paranotal theory*, first proposed by Müller (1873, 1875) and strongly supported by Crampton (1916), dominated the field for more than 50 years and is still advocated by some recent workers. The so-called 'gill theory' of Gegenbaur was resurrected by Wigglesworth (1976), and Kukalová-Peck (1978, 1983, 1987) provided ample evidence for the rejection of the paranotal theory. The most plausible alternative, proposed by Kukalová-Peck (1983), involves the origin of wings from leg-based appendages, epicoxal exites probably homologous to the exites of Crustacea (see Chapter 6). The original function or functions of these proto-wings and the steps that led to the development of flight have been the subjects of lively debate (see Wootton 1986).

Once wings became functional flight organs, almost endless possibilities arose for further modification. Thus, the mesothoracic pair became modified into protective *tegmina* in the blattoid and orthopteroid orders, *hemelytra* in the heteropteran Hemiptera, and *elytra* in the Coleoptera. This division of function led to concentration of the propulsive drive and at least most of the lift in the hind wings, and the process was carried further in groups with reduced tegmina or elytra. On the other hand, reduction of the hind wings in many insects led to improved aerodynamic efficiency in the fore wings, and the same advantage underlies the evolution of various methods of coupling the fore and hind wings together. Nevertheless, the ancient Odonata became highly efficient fliers without coupling, by developing excellent aerofoils and a remarkable degree of neuro-muscular control. Still another series of specialisations is seen in small insects that take advantage of rising air currents and are dispersed in an 'aerial plankton'. They tend to have small wings, reduced venation, and marginal fringes of long hairs. Probably the most remarkable modification of all is the transformation of the wings into paddles in the males of a marine midge. Finally, wings may lack selective value in insects that have adopted a sedentary, cryptic or parasitic way of life, or that live in montane, insular or high-latitude habitats, and we find *brachypterous* (short-winged) and *apterous* (wingless) forms in almost every order of the Neoptera.

Apart from, or perhaps associated with, their great adaptive significance, the wings of insects show so many characters of value in classification that they have been used more extensively than any other structure in compar-

ative studies. Their importance is the greater, because they are usually the only remains of insects that are recognisably preserved in fossils, which often show essential details, even down to the chaetotaxy, with remarkable clarity.

Structure and Topography of the Wings

During development, the wings are flat, lightly sclerotised bags, lined by epidermis, filled with blood, and containing nerve fibres and tracheae. The veins are laid down as bands of pigment in the cuticle. Those on the morphologically dorsal surface give rise to 'convex' veins which come to lie on ridges in the completed wing, and those on the ventral surface give rise to 'concave' veins lying in hollows or furrows. When the wing has expanded and dried after emergence of the adult, it becomes a membranous sheet, with the two layers of cuticle closely approximated, except where they are separated by the sclerotised tubes that form the strengthening and supporting veins. The more or less regular alternation between convexity and concavity in the arrangement of the veins (veinal fluting) is a further strengthening mechanism.

The membrane may be clear or marked by a pattern of pigment, and there is often a sharply defined, opaque or pigmented area, the *pterostigma*, near the distal end of the anterior margin. Hairs on the wings are of two kinds (Fig. 1.15): *microtrichia* (*aculeae*), which are very small, and irregularly scattered over membrane and veins or gathered into diffuse patches; and *macrotrichia*, which are larger, provided with sockets, and often restricted to the veins. The *scales* on the wings of Lepidoptera, Trichoptera and some Diptera and Psocoptera are flattened and striated macrotrichia.

The wing is treated morphologically as being held in the horizontal plane at right angles to the long axis of the body. It is approximately triangular in shape, and its borders can be defined as *anterior* or *costal margin*, *posterior margin* (*outer margin* or *termen*) from the apex to the *anal angle* (*tornus*), and *anal margin* (*inner margin* or *dorsum*) from there to the base (Fig. 1.16). A (*humeral*) angle may be recognised when the costa curves sharply backwards at the base of the wing anteriorly. The wing may be divided into topographical areas. At the base, there is a triangular *axillary* area containing the articular

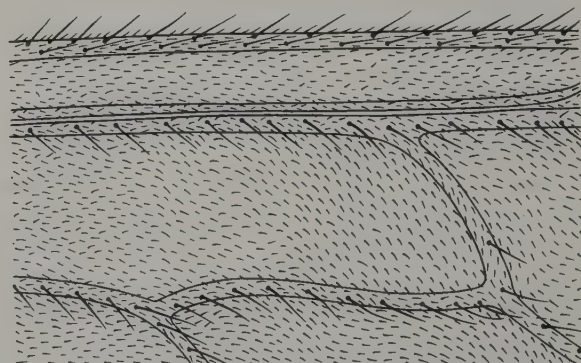


Fig. 1.15 Portion of fore wing of *Caecilius* sp. (PSOC), showing macrotrichia and microtrichia.
[B. Rankin]

sclerites (see below). The main part of the wing, chiefly responsible for maintaining and propelling the insect in flight, is called the *remigium*. It is separated by a *claval fold* or *furrow* (lying just behind CuP) from the more or less triangular *anal* (or *ano-jugal*) area, which is, in turn, divided by the *anal fold*, in between AA and AP (Fig. 1.18). The fourth area, less constantly present, is a much smaller *jugal area* (*neala*), separated by a *jugal fold*, and lying between the anal area and the base of the wing posteriorly. The term *vannus* or *vannal area* is often used for the expanded anal area in the hind wings of many insects. These areas and the divisions between them are important in relation to the folding of the wing at rest, as well as to the flexion of its different parts in flight, and they are also useful in defining the limits of the venational fields. Wootton (1979) reviewed the nomenclature of the wing components from a functional point of view, distinguishing between *flexion-lines* and *fold-lines* and redefining some of the areas.

Basal Attachment

The attachment of the wings to the thorax is somewhat complicated, in conformity with the fact that their movements are rather precisely limited and are produced in two different ways. Vertical flapping movements are generally produced by distortion of the notum through the action of the indirect muscles; other movements, including antero-posterior and rotational movements, as well as those that bring the wing into the resting position in the Neoptera, are performed by the so-called *direct wing muscles*; these include the *axillary muscles*, originating on the pleuron and inserting on the articular sclerites (see below), and the *basalar* and *subalar muscles*, associated with the *basalaria* and *subalaria*, respectively (see below). The mechanisms of attachment differ appreciably in the Palaeoptera and Neoptera, and these have been homologised by Kukalová-Peck (1983) (see Chapter 6). According to her scheme, the ancestor had a row of 4 *articular sclerites* (*proxalare*, *axalare*, *fulcalare* and *basivenale*) aligned with each of the 8 primary wing veins, thus forming a densely crowded band of 32 sclerites (4 columns and 8 rows) (Fig. 6.10); lying below this band were 2 sets of *epipleurites*, the anterior *basalaria* (sing. *basalare*) and the posterior *subalaria* (sing. *subalare*). The *articular plates* of Palaeoptera and the *axillary sclerites*, *humeral plate* and *median plate* of Neoptera represent various composite clusters of these original sclerites (see below). Living Pterygota have three

distinct types of wing articulation: ephemeropteran, odonatan and neopteran, which are discussed below.

In the Odonata (Fig. 1.17A) the wing has two large basal plates, the *anterior axillary plate* ('humeral plate') anteriorly, to which the costal vein is articulated by means of its basivenale (usually called the 'intercalated piece') and the *posterior axillary plate*, to which the remaining main veins are fused. The anterior plate also incorporates the *basalaria*, which are fused to it ventrally. The two axillary plates articulate, somewhat loosely, with each other, with one column of separate sclerites (*proxalaria*) on the lateral edge of the notum dorsally, and with separate fulcral arms of the pleural wing process ventrally. As a result, flapping movement is unimpeded, deflection of the costal margin (important in flight control) is moderately free, and the small movements in other directions that are needed for stability and manoeuvrability can be made. The wings cannot be folded backwards over the abdomen, but can only be raised upwards or held in a permanently outstretched position (Fig. 17.3; Plate 1); in nearly all Zygoptera and a very few Anisoptera, however, the oblique orientation of the pterothorax allows the wings to be brought together and positioned in an antero-posterior direction.

The Ephemeroptera (Fig. 1.17B) have the articulated costal basivenale ('intercalated piece') as in Odonata, but they lack the anterior axillary plate. The posterior axillary plate is narrower than in Odonata; there are two columns of articular sclerites (*proxalaria* and *axalaria*) at the lateral edge of the notum (some of which are desclerotised in modern forms); and the wings can be raised upwards (Fig. 16.1) as in Odonata.

The Neoptera (Fig. 1.17C) can perform the same flight movements as the palaeopteran pterygotes, but (except in a few forms with secondarily limited movement) they can also fold the wings back along the abdomen, sometimes with extensive pleating of an enlarged anal area. The wing articulates dorsally with the *anterior* and *posterior wing processes* (*proxalaria* closely associated with or fused to the notum) and rests ventrally on the pleural wing process (at the upper end of the junction between the episternum and epimeron, Figs 1.11A, B) and on the *epipleurites* (*basalare* and *subalare*), thus forming a fulcrum (or series of fulcra) at the upper end of the pleuron. The articulation between the wing and the wing processes is mediated by a series of separate, movable *articular sclerites* (*pteralia*) consisting of: a *humeral plate* (costal basivenale and fulcalare fused together) basal to the costa; the *tegula*, a scale-like sclerite basal to the humeral plate in the fore wing only; and the *axillary sclerites* (representing fusions of original clusters of sclerites discussed above and in Chapter 6): the *1st axillary* (1Ax) between the anterior wing process and the subcostal basivenale; the *2nd axillary* (2Ax), articulating partly with the 1st axillary, partly with the radial basivenale, and ventrally with the pleural wing process; and the *3rd axillary* (3Ax), articulating with the posterior wing process (anal and jugal *proxalaria*) or the 4th axillary (when these *proxalaria* are free from the notum) and the anal and jugal *basivenalia*. A wing flexor muscle between 3Ax and the pleuron

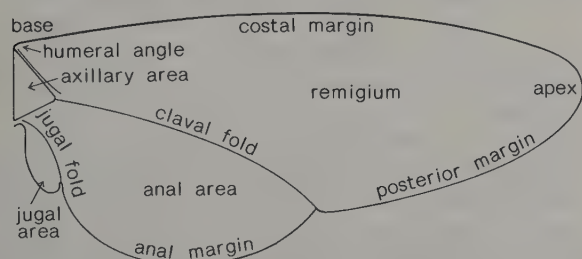


Fig. 1.16 Topography of an insect wing (diagrammatic). The 'lateral' margin is often better referred to as posterior or posterolateral.

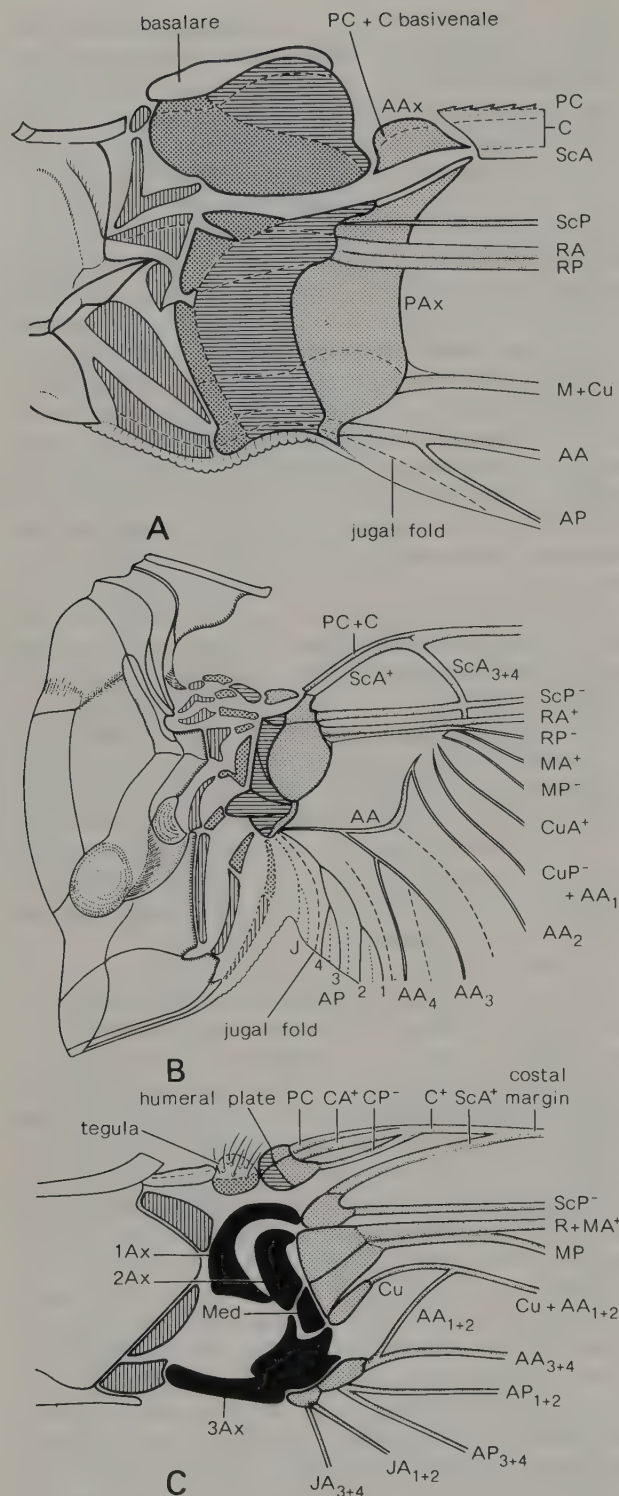


Fig. 1.17 Basal articulation of the wing (diagrammatic): A, Odonata; B, Ephemeroptera; C, Neoptera. Dotted lines indicate sclerites or sutures present in fossils but absent in extant forms. Shading has been used to indicate homologies (1) between the one (proxalaria) or two (proxalaria and axalaria) columns of articular sclerites in Palaeoptera and the anterior and posterior wing processes (proxalaria) of Neoptera, and 2) between various elements derived from one or more basivenalia (see Figs 6.12a, 6.16 for details). AAx, PAx = anterior, posterior axillary plates; Med = medial plates; 1Ax, 2Ax, 3Ax = 1st, 2nd and 3rd axillary sclerites.

[J. Kukalová-Peck; S. Smith]

is responsible for the flexion of the wing back over the abdomen. A *median plate* (medial fulcalare) lies between the 2nd and 3rd axillaries, and a second median plate is sometimes formed by the combined basivenalia of the radial, medial and cubital veins. The membrane at the base of the wing posteriorly is usually thickened to form an *axillary cord*. The costal margin can rotate backwards at the joints provided by the humeral plate, and the 3rd axillary can pivot and rotate, producing a sharp fold between the basivenalia and the axillaries and a crumpling of the wing basal to them, so that this part of the wing folds up as the rest of it is drawn back.

Coupling Mechanisms

A slow, irregular flight of unpredictable direction has certain advantages in protecting against fast-moving predators, as anyone who has chased butterflies knows; but there are also advantages in improved aerodynamic efficiency leading to higher speeds and a greater range of flight in relation to available energy reserves. As already mentioned, this has been achieved in various ways, and we are concerned here with the methods of coupling the fore and hind wings together that have been evolved independently in several orders.

In the Hymenoptera a sclerotised fold along the posterior margin of the fore wing is engaged by a row of small hooks (*hamuli*) on the anterior margin of the hind wing, giving the *hamulate* type of coupling, which is also more or less developed in some Trichoptera and a few other groups. In some Hemiptera the wings are held together by a variety of small hooks or folds along the margins, and in the Psocoptera the costa of the hind wing is held by a spiny or hooked process at the node in the fore wing where vein CuP reaches the margin. Complex and varied couplings are developed in the mecopterid orders (Tillyard 1918a, 1919d), in which the jugal area of the fore wing is often developed into a *jugal lobe* ('fibula' in Lepidoptera, 'alula' in Diptera), and the anterior margin of the hind wing, when present, is produced into a small *humeral lobe* near its base. In the simplest condition these lobes merely overlap, and an extension of this process over a wider area produces the *amplexiform* method of coupling. In Mecoptera both lobes may bear long bristles, the jugal bristles lying on top of the hind wing in flight, while the humeral bristles form the *frenulum* which presses against the underside of the fore wing. In some Trichoptera and lower Lepidoptera the jugal lobe is produced into a projecting *jugum*. (For the varied methods of coupling in Lepidoptera see Chapter 41.)

Wing Venation

Four criteria have been used in assessing the homologies of the veins:

(1) The classical method used by Comstock and Needham (Comstock 1918) was to follow the tracheation in the developing wing-sheath. The assumption was that tracheation determines the positions of the veins and, in juveniles, recapitulates the ancestral adult venation. In many insects the tracheae enter the wing in two main trunks, an anterior *costo-radial* and a posterior *cubito-*

anal and then divide to enter the veinal branches. The limitation of this method is that the lacunae preceding the formation of the wing veins function primarily as blood channels (Arnold 1964), and the tracheae and nerves grow into these channels only after the venational pattern has been established. It has been shown by Whitten (1962) and others (see references in Kukalová-Peck 1978) that tracheal systems may differ from one instar to another in connection with specific functional requirements, and that pupal tracheation may differ considerably from that of the adult. The positions of tracheae are often opportunistic, and there is no developmental evidence for fusion or migration of tracheae.

(2) Tillyard (1918a) made use of the fact that macrotrichia are often limited to main longitudinal veins and their branches. There are many exceptions, and the method seems to have most use in indicating where veins may have disappeared.

(3) There is a strong tendency for main veins to be alternately 'convex' and 'concave', especially towards their bases, and they are often denoted, respectively, by plus and minus signs (Fig. 1.18). This condition is undoubtedly primitive, and it is of considerable practical value in identifying veins and determining their homologies. Its limitation is that veins respond to mechanical need, and the level of some veins, particularly of their distal portions, may become altered (e.g. concave to neutral or even convex, as in branches of RP and MP in most Neoptera) in response to changing needs in the course of evolution. Veins may also change from + to - or from - to + as a result of being 'captured' (by superposition) or replaced by a vein of the opposite sign.

(4) The final court of appeal is a careful study of comparative morphology within groups and between groups, including the evidence that can be obtained from fossils. Generalised members of an order rarely present serious difficulty; it is when the venation is reduced or distorted that it may become difficult or impossible to apply any consistent notation to it. It is crucial to establish a correct *groundplan* (see p. 117) based on primitive venation, since primary veins, once lost, are never regained. Only secondary venation (cross-veins, sclerotised folds, intercalated veins, struts, networks or pigmented areas serving as reinforcements or binding patches) can be formed from the wing membrane.

An historical scenario of wing origin and evolution has been developed by J. Kukalová-Peck, based on evidence from both fossil and Recent insects (see Chapter 6). According to this scenario, wing precursors or *proto-wings* of the ancestors of the pterygotes first became fissured for more flexibility into dichotomously branched sections, similar to the leg-based appendages of Crustacea (e.g. telson plates). The cuticle in between these proto-veins formed a dense, irregular network called the *archedictyon* which has been preserved in a few primitive groups (e.g. Fig. 19.10). The early proto-wing had 8 veinal pairs, each arising from a subdivided *basivenale* (pl. *basivenalia*) which served as a blood sinus. Each pair diverged immediately at the base into an anterior convex sector and a posterior concave one. Later, the two sectors

often became fused into *veinal stems* near the wing base. Aerodynamic requirements necessitated the crowding together of the anterior veins to strengthen the forward edge and produce an asymmetrical air foil. Various braces and fusions between veins (e.g. AA₁₊₂ & CuP or Cu, MA & R or RP, MP & Cu or CuA) evolved many times in parallel as reinforcements of sections of the wing (particularly near the base). The archedictyon either formed cross-veins or disappeared in most insects. The subsequent evolution of wing venation is, in general, marked by reduction. Only rarely in enlarged forms has supplementary venation developed from the wing membrane.

The differences in interpretation of vein homologies that have developed over the years are of great theoretical importance, but they have usually involved only minor changes in notation. The names of the major veins utilised in the present text (*costa*, *subcosta*, *radius*, *media*, *cubitus* and *anal*) are the same as those used in the classical works of Redtenbacher (1886), Comstock (1918), Lameere (1922) and Martynov (1925), two more names being added by later authors for reduced veins at the anterior (*precosta*) and posterior (*jugal*) ends of the wing. The latter are well-developed only in fossils and a few extant groups. The details of wing nomenclature, however, differ considerably, even in more modern works (Snodgrass 1935; Hamilton 1971b-72c; Wootton 1979; Kukalová-Peck 1983, 1987). The system used in this chapter and in Chapter 6 is that of Kukalová-Peck, but different systems may be employed by authors dealing with specific insect orders. This venational scheme differs from others in being based on a groundplan of 8 veinal pairs, each with a convex (+) and concave (-) sector. A generalised neopteran wing is illustrated in Figs 1.18A and B contrasting the present terminology with that used in the 1st edition.

Precosta (PC). This vein is fused with the costa in all extant insects. In Odonata it is still recognisable as a serrated strip; in Auchenorrhyncha (Hemiptera) it may be expanded basally in the fore wing; and in Coleoptera it forms the elytral epipleuron.

Costa (C). This vein is usually convex, strong and marginal; it generally extends to the apex of the wing and may be continuous with a delicate *ambient vein* (a secondary development) around the posterior margin. In most Recent insects, the anterior and posterior sectors fuse together almost immediately at the base. CP- is well preserved in some Auchenorrhyncha (Cicadoidea) and may resemble a 'subcosta' with serial veinlets.

Subcosta (Sc). This is mainly represented by its posterior sector (ScP-), which lies in a deep furrow between the costa and radius. It sometimes sends off a series of secondary veinlets. The anterior sector (ScA+) forms an oblique brace between the subcostal basivenale and costal margin and may be long and conspicuous in some Orthoptera, arched in Ephemeroptera, or strongly inflated in Neuropterida. Sc is reduced or fused to R in most Hemiptera.

Radius (R). The *radius anterior* (RA+) is generally the strongest vein in the wing and with the *radius posterior* (RP-) covers the largest portion of the wing apex. RA may be unbranched or form the terminal branches RA₁₊₂

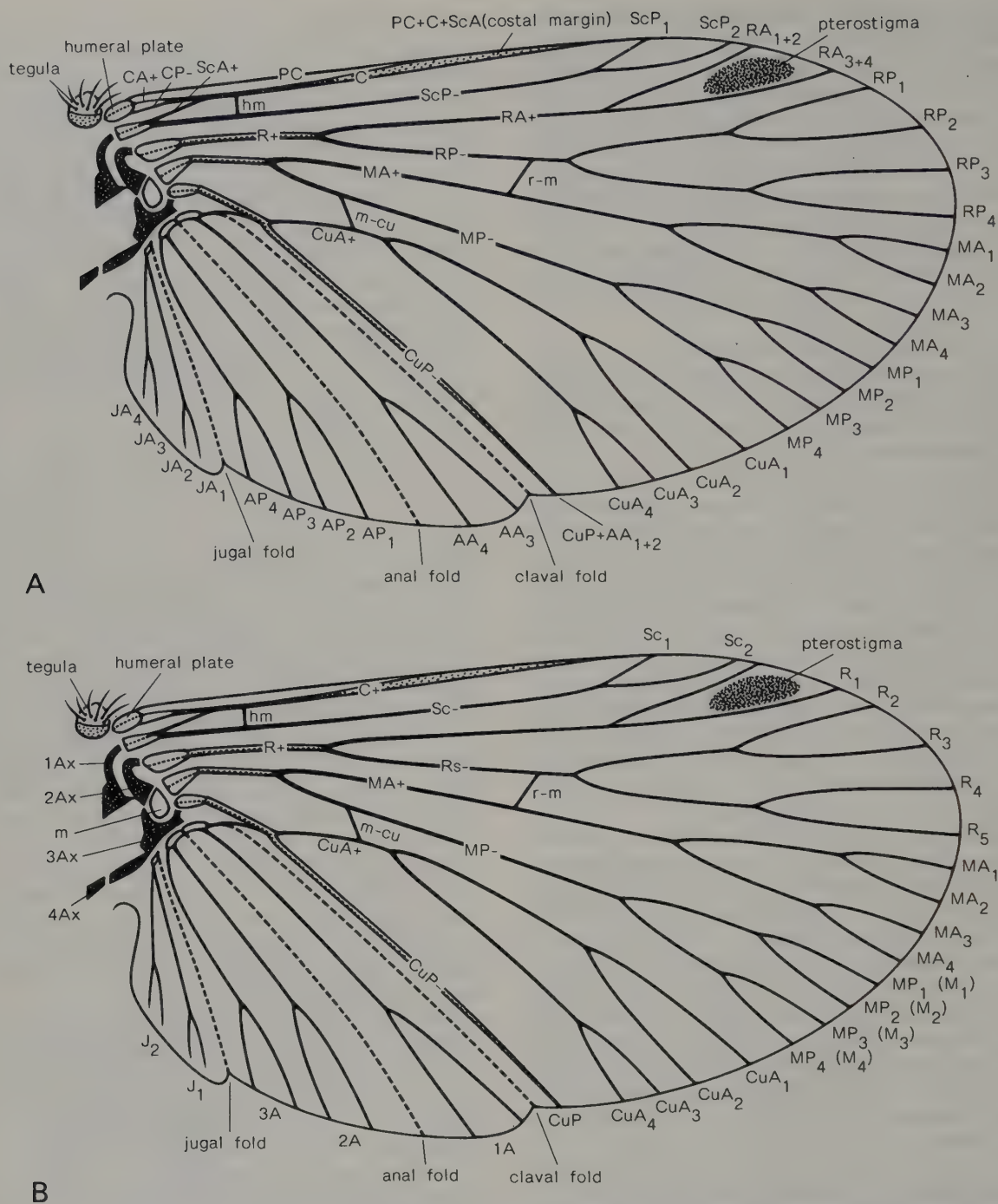


Fig. 1.18 Wing venation (diagrammatic): A, terminology adopted in this chapter; B, terminology used in the 1st edition, with some alternate designations occurring in the literature. [J. Kukalová-Peck; S. P. Kim]

and RA_{3+4} , with the pterostigma between them, while RP normally divides twice to produce 4 terminal veins, RP_{1-4} . Usually, RP separates from RA far from the base of the wing, but sometimes (in Odonata and Ephemeroptera) both sectors arise directly from the subdivided radial basivenale. RP is often referred to as the *radial sector* (Rs) and the end branches of the radius are often numbered R_{1-5} .

Media (M). The *media anterior* (MA+) and *media posterior* (MP-) are usually relatively strong and 4-

branched. MA is well-developed in Palaeoptera and in some Orthoptera, but in blattoids, hemipteroids and endopterygotes it has become fused with R at the base of the wing, so that MP alone occupies the medial area (see Chapter 6). Where this has happened the branches are sometimes referred to as M_{1-4} . In Neoptera, MP is frequently connected with CuA of Cu by a brace formed by a cross-vein or a fusion; this was called 'M₅' by Tillyard (1919d).

Cubitus (Cu). The *cubitus anterior* (CuA+) is another

strong vein, which may divide distally forming 4 or fewer branches. The *cubitus posterior* (CuP-) is usually unbranched, often lies in the claval furrow of the wing, and is sometimes reduced, especially in the hind wings of some Endopterygota and the fore wings of Heteroptera (Hemiptera).

Anal (A). This vein often forks close to its basivenale to form AA and AP, both of which are forked; the two sectors are frequently separated by the anal fold. In Neoptera, AA or its anterior branch is always fused with or adjacent to Cu or CuP, forming an *anal brace*. AA or AA₁₊₂ may also be cut off from the anal basivenale by a fold, so that it appears to arise from the cubital basivenale; this led to the vein being called 'postcubitus' by Snodgrass (1935) and 'empusal' by Hamilton (1971b-72c). Anal branches are all convex, even if derived from the original AP-, except in a few Odonata where the concave condition persists. In hind wings with a very wide, sharply defined anal area or vannus, as in most orthopteroid orders, the anals branch several times creating a fan-like appearance; for this reason they were called 'vannals' by Snodgrass (1935).

Jugal (J). This vein may be represented by one or two small veins in the jugal area at the base of the wing; these have sometimes been referred to as the 'arcuate' and 'cardinal' veins. Jugal veins were originally present in both Palaeoptera and Neoptera, but they are reduced in extant palaeopterans.

The generalised arrangement shown in Fig. 1.18 involves a simple *dichotomous* branching of the veins, but two other types of branching also occur (Fig. 1.19). One is *pectinate*, in which a number of branches come by migration to lie serially along a single stem. The other, called *triadic* by Tillyard, is extensively developed only in the palaeopteran pterygotes among Recent insects. It consists of the interpolation of a longitudinal vein between the pairs of branches of the main veins. The intercalated vein is of opposite sign to those between which it lies, and the group is called a positive triad when a concave vein is intercalated between two convex branches, and a negative triad when a convex vein is intercalated between two concave ones.

In addition, there may be considerable terminal branching beyond the basic amount already described, and short, secondary branches (*veinlets*) may diverge from the main veins. The *humeral vein* (hm) near the base of the costal area of the wing and the series of veinlets on the subcosta are the most important examples of this class. *Cross-veins* are transverse struts, which are rarely penetrated by tracheae, and which strengthen the wing by joining longitu-

dinal veins together. They vary in number and position, and are indicated by lower-case italic letters hyphenated together (for example, *r-m* between the radial and median areas or *r-r* between 2 branches of the radius). Some cross-veins that are relatively constant in occurrence and position are shown in Fig. 1.18.

Finally, those areas of the wing membrane locally delimited by longitudinal and cross-veins, or by confluence of two longitudinal veins, are called *cells*, and they are often designated by letters and figures corresponding to the veins or portions of veins behind which they lie. Special cells, such as the 'median' (or 'discal') and 'basal' cells, are usually indicated by name, and it is not to be forgotten that these terms are used for different cells in different orders.

ABDOMEN

The abdomen (Fig. 1.20) consists primitively of eleven segments, although the first is often reduced or incorporated in the thorax, and there may also be reduction at the caudal end. The first eight segments are generally of broadly similar architecture. Each is strengthened by a more or less arched tergal plate and a smaller, flatter sternal plate, separated from each other by a relatively wide expanse of pleural membrane, and the conjunctival membrane between consecutive plates is also relatively extensive. Consequently the abdomen is normally more mobile, and certainly more distensible, than the other parts of the body. The occurrence of true (albeit short) abdominal limbs on the pregenital segments is commonplace in the apterygote grade, but it remains debatable whether any of the abdominal appendages found in a number of neopteran immatures are derivatives of the segmental limbs or whether they are neoformations. Spiracles are normally present on the pleura or sterna of segments 1 to 8, but may be reduced, or incorporated in lateral extensions of the terga. The endoskeleton consists of tergal phragmata. In some groups the first four or five segments are developed into a more or less globular *pre-abdomen* with rather closely united terga, the remainder forming a tubular, retractile *postabdomen*. The Hymenoptera show some remarkable modifications in the size and shape of the segments, and the first is fused with the thorax in the Apocrita (Fig. 42.10c).

Terminalia

The segments from 8 or 9 (occasionally from 7) to the end of the abdomen are modified and more or less combined to form an ano-genital tagma, which may be

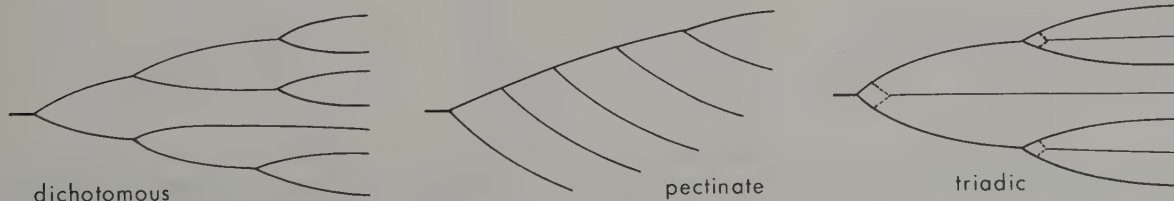


Fig. 1.19 Types of branching of wing veins.

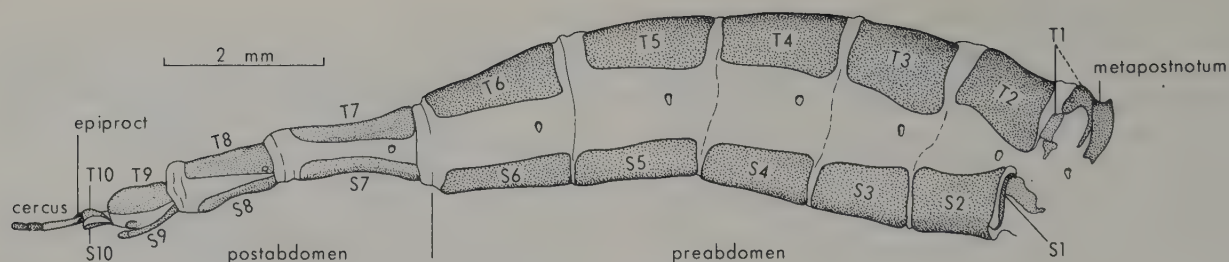


Fig. 1.20 Abdomen of *Chorista australis* (MECO), ♀, from a cleared preparation with segments fully extended.

referred to as the *terminalia*, the genital parts being the *genitalia*. Descriptions of these structures in the different orders have been published by a number of authors in Tuxen (1970b). Both the male and female terminalia have been widely used in taxonomy, particularly as aids in distinguishing between species, and in some genera the only clearly recognisable specific characters are to be found in them.

Excretory and sensory adaptations of the terminalia do not, in general, differ greatly between the sexes or in different groups of insects, but the reproductive adaptations do. Insects almost certainly evolved from ancestors in which internal fertilisation was achieved by indirect transfer, the females picking up spermatophores deposited by the males. This method has survived in the apterygotes. True copulation (i.e. direct transfer of spermatophores or free spermatozoa by apposition of specialised genital structures) probably evolved at least twice in the Pterygota: by the development of an intromittent organ on abdominal sternum 2 (S2) of the male in Odonata; and by specialisation of the terminalia in all other orders. The primitive mating position in these orders appears to have been with the male beneath (or at the side), but the evolution of a male intromittent organ and efficient holding devices led to the adoption of other positions (male-above, end-to-end) (Alexander 1964).

The accessory structures that were available to become adapted for reproductive functions can be appreciated best

on the theory, for which there is a good deal of evidence, that the ancestors of the insects had reduced abdominal limbs (Fig. 1.21B), with coxal styles at their bases and eversible (exsertile) vesicles mesal to them, the basic plan being similar to that of the Symphyla (Fig. 1.21A). In Archaeognatha segments 8 and 9 of the abdomen (Fig. 1.21C) have well-defined coxites (*gonocoxites*), each with a *gonostyle*, and often an additional pair of styliform appendages, but apparently no vesicles. There has been considerable confusion, because the term 'style' has been used indiscriminately for both kinds of appendage, but the most plausible explanation is that the distal, more lateral pair on each segment are rudimentary limbs (*telopodites*) and the mesal pair are true coxal styles. The latter may be distinguished as *gonapophyses*, but the term 'style' (or *gonostyle*) has become so widely used for the former that its continued employment cannot now be avoided. No definite appendages have been detected on segment 10 of any primitive insect. A general review of insect genitalia was published by Scudder (1971).

Female

The functions of the female terminalia are to receive spermatozoa, to deposit eggs in appropriate situations, sometimes (Blattodea, Mantodea) to form an ootheca, occasionally (viviparous species) to accommodate a developing embryo or larva, to dispose of waste products, and to serve as a base for posterior sense organs.

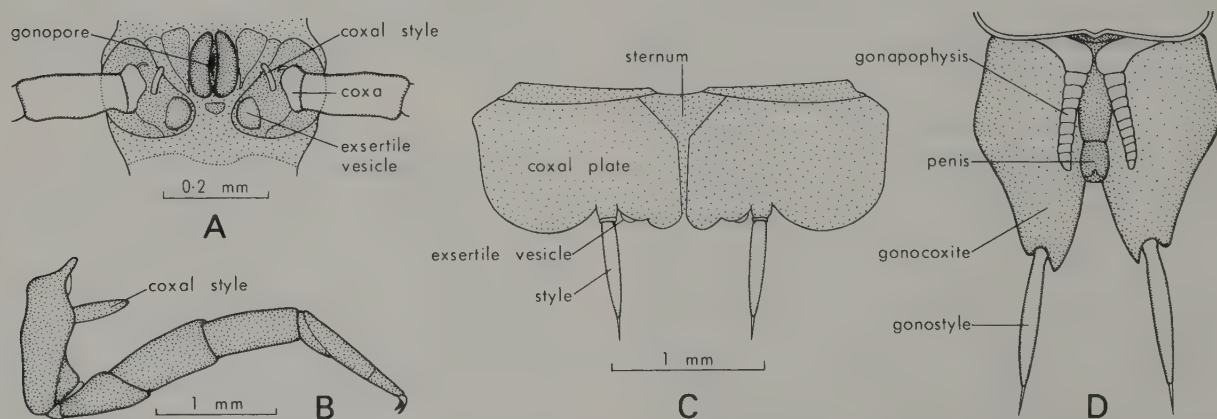


Fig. 1.21 A, 4th trunk segment of *Hanseniella* sp. (Symphyla), ♂, ventral, with functional limbs, coxal styles and eversible vesicles; B, mid leg of *Allomachilis froggatti* (ARCH), ♀, posterior, with coxal style (no eversible vesicles on thorax); C, mid-abdominal segment of *A. froggatti*, ventral, with coxites incorporated into sternum, styles (rudimentary distal segments of limb) and eversible vesicles; D, 9th (genital) segment of *Machilis variabilis* (ARCH), ♂, with coxites, gonostyles and gonapophyses, but no exsertile vesicles.

[After Snodgrass 1957]

Modifications to aid the male in clasping are not uncommon on other parts of the body, but are generally inconspicuous in the genital segments. The *gonopore*, which is the opening of the distal (usually secondary) part of the common oviduct, is in the median line behind sternum 7 (S7) in Ephemeroptera and Dermaptera, S8 or S9 in other insects, sometimes on the surface, but commonly at the bottom of a more or less deeply invaginated *genital atrium* or *vagina*, the external opening then being known as the *vulva* (Fig. 1.22). The spermathecal duct and accessory glands usually open into the atrium. The *anus* is on segment 11, which may become incorporated in 10.

In apterygotes (Fig. 1.23), segments 8 and 9 have well developed coxites, styles and gonapophyses, the two pairs of gonapophyses being closely applied together to form an *ovipositor*; segment 10 is complete; segment 11 is small, the tergum forming a mid-dorsal *epiproct*, and the sternum being partly divided into a pair of ventral *paraprocts*; the anus is surrounded by three small papillae. The *cerci* are articulated to segment 11 laterally, and a median *appendix dorsalis* ('caudal style') arises from the distal end of the epiproct just above the dorsal anal papilla. This is a remarkable appendage, which is found in the apterygotes, some Palaeodictyoptera and most Ephemeroptera. Within the Neoptera, an appendix dorsalis is only reported as 'filum terminale', from Austroperlidae (Plecoptera) nymphs (Illies 1965), but this could also be a neoformation. Its significance in the evolution of the insects is obscure.

In the Pterygota, the appendages of segments 8 and 9 are reduced, and the ovipositor consists of three pairs of *valves*. In some Odonata (Fig. 1.24A), for example, the gonocoxites of segment 8 are reduced to a small sclerite (*anterior* or 1st *valvifer*) on each side, with a long process (*ventral*, anterior or 1st *valve*) representing the gonapophysis, and no gonostyle. The gonocoxites of segment 9 are elongate; their bases are the *posterior* or 2nd *valvifers*, their distal parts the *dorsal*, lateral or 3rd *valves*, with a subapical style, and the gonapophyses the *medial*, posterior or 2nd *valves*. Scudder (1961) has noted that a detached piece (gonangulum), probably derived from the base of the 9th-segment coxite, is constantly present, and

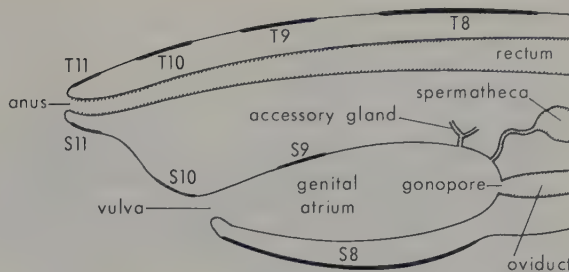


Fig. 1.22 Terminal abdominal segments of a generalised ♀ neopteran (diagrammatic median sagittal section with appendages omitted; see Fig. 19.3A).

replaces, or fuses with, the 8th-segment coxite as the anterior valvifer in some orders; he also proposed the term *gonoplac* for the dorsal valves. Except for loss of the style, the structure is basically similar, however widely the functional requirements may vary, in Orthoptera (Fig. 1.24B) and other groups (auchenorrhynchan Hemiptera, terebrantian Thysanoptera, Hymenoptera) that have retained a well-developed ovipositor. In Blattodea, a large genital atrium is formed by infolding of sternum 8 (S8), the surface of which is modified as a mould for the ootheca, and the valves are considerably reduced.

The segmental structures are retained only to the extent that they perform a specific function. Thus, the appendages of segments 8 and 9 are greatly reduced or lost in Ephemeroptera, many Odonata, Plecoptera, Isoptera, most hemipteroids and most endopterygotes; segments 10 and 11 are compacted in representatives of many orders, though the epiproct and paraprocts usually remain recognisable; and cerci are absent in hemipteroids, and reduced or rudimentary in endopterygotes. Fig. 1.24C shows a type found in many panorpoid terminalia.

In the Ephemeroptera, sternum 7 (S7) is sometimes produced posteriorly to form a *subgenital plate*. The subgenital plate is formed by S7 in Blattodea also (S8 being inflected), but by S8 in most other groups in which it is differentiated. Tergum 10 or 9 (or both) may be divided into *hemitergites* by a median cleft, either may form a *supra-anal plate* over the anal segment dorsally, and the

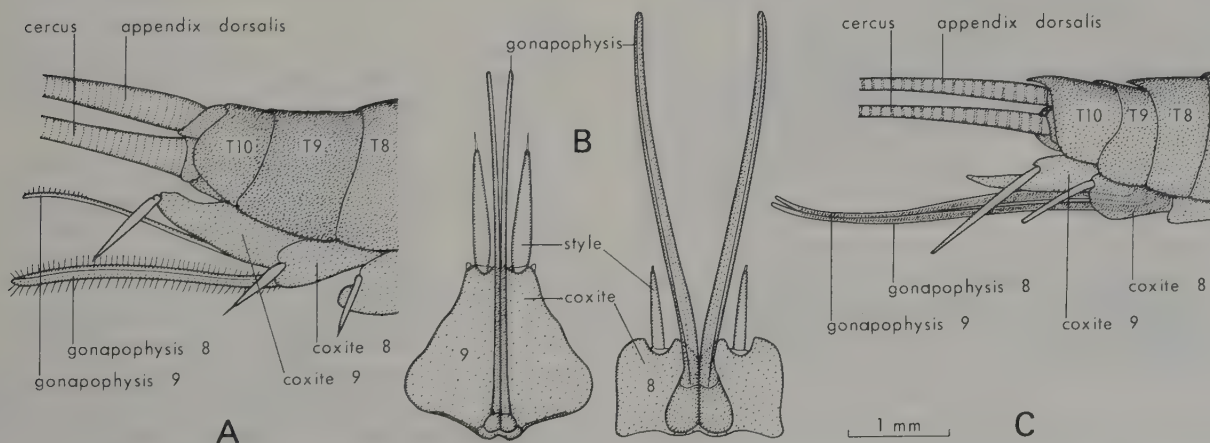


Fig. 1.23 Female terminalia of Apterygota: A, *Allomachilis froggatti* (ARCH), lateral; B, appendages of 9th and 8th segments of same, dorsal; C, *Ctenolepisma longicaudata* (THNU), lateral.

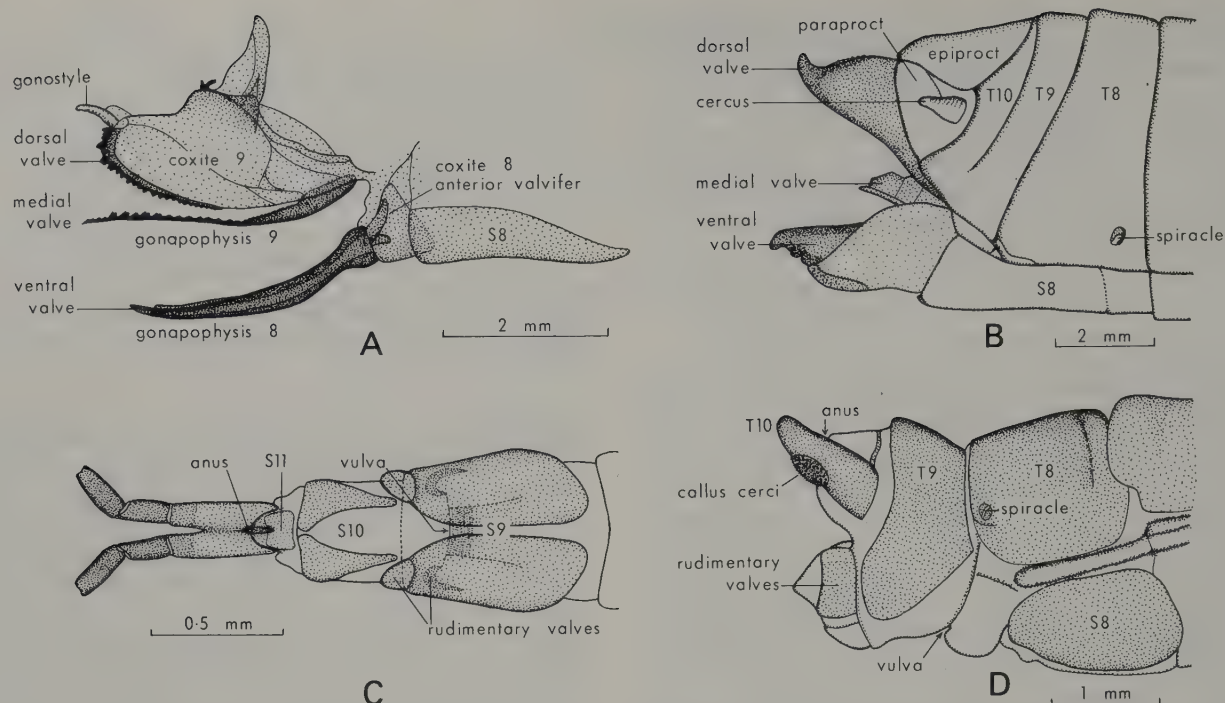


Fig. 1.24 Female terminalia of some Pterygota: A, ovipositor of *Synlestes weyersii tillyardi* (ODON), dissected (for normal position of parts see Fig. 17.6); B, *Gastrimargus musicus* (ORTH), lateral; C, *Chorista australis* (MECO), ventral (the rudimentary appendages of S9 presumably represent the median dorsal valves); D, *Archichauliodes guttiferus* (MEGA), showing reduction and compaction.

corresponding sternites may be reduced or absent. An endoskeletal furca may also be developed as a separate internal sclerite. An extreme modification is seen in the Lepidoptera, in which there may be two genital openings (one for copulation, one for oviposition), or they may be combined with the rectum in a common cloaca opening at the end of the body.

Male

The functions of the male terminalia are to maintain apposition with the genital opening of the female during copulation, often to construct spermatophores, to inject spermatophores or semen into the genital tract (occasionally into the haemocoel) of the female, and to perform excretory and sensory functions as in the female. So far as the structures are concerned, there is endless confusion in terminology (see Tuxen 1970b) and sharp disagreement on homologies. It is consequently difficult to present a clear picture of evolutionary sequences. The Odonata, as already mentioned, have a different method of copulation from other insects, and their genitalia are described separately in Chapter 17.

The enormous complexity in both clasping and intro-mittent organs in arthropods (and in many other animal groups) has been of great interest to biologists, and various hypotheses have been presented to explain genitalic evolution. The most recent and most plausible of these is that of Eberhard (1985), who concludes that females discriminate among males of their own species on the basis of sensory stimuli produced by the genital organs. The genitalia are thus involved in a type of 'internal courtship'

which varies in its effectiveness in eliciting the proper female responses (e.g. completion of the act of copulation, transportation and storage of sperm, ovulation and egg maturation and insemination).

The males of a few Archaeognatha (Fig. 1.21D) have gonocoxites, gonostyles and gonapophyses on both segments 8 and 9, and are consequently like females, except that a membranous median *penis* (or phallus) projects backwards between the posterior gonapophyses. In most apterygotes (Figs 1.25B, C) the 8th-segment coxites are relatively small and without gonapophyses, and the penis of Thysanura tends to be bilobed and sometimes contains separate ejaculatory ducts. The terminal segments and appendages are similar to those of the female. That the differences between the sexes are so slight presumably is associated with the absence of complete copulation, the male producing a thread beaded with sperm droplets, and simply guiding the vulva of the female into contact with it by means of an antenna or cercus.

The Ephemeroptera (Fig. 1.26) probably show the most primitive method of aerial mating in recent Pterygota (Brinck 1957). The male approaches the female from below, hooks his long, 'double-jointed' fore tarsi over the bases of her wings, which he steadies with his cerci, grasps her abdomen with his 'forceps', and inserts his penes into her vulva from below and behind. There are no appendages on segment 8 (nor in any pterygote males); the gonocoxites of 9 often have segmented styles (Fig. 1.25D); there are usually two penes containing separate ejaculatory ducts; and there are sometimes associated processes which may be gonapophyses. Segment 10 is well

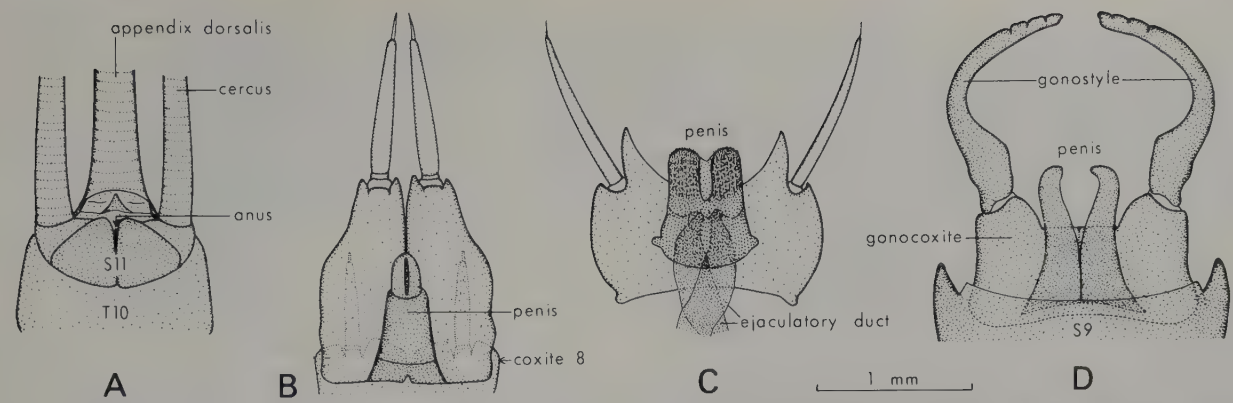


Fig. 1.25 Male terminalia: A, terminal segments of *Allomachilis froggatti* (ARCH), ventral, with S10 and underlying structures removed; B, segment 9 and penis of *A. froggatti*, dorsal; C, same of *Ctenolepisma longicaudata* (THNU); D, same of *Mirawara aapta* (EPHE), with fused gonocoxites.

developed, 11 is represented by a small epiproct and separate paraprocts, and the cerci and appendix dorsalis are usually long. The similarity of the apparatus to that of the apterygotes is evident.

A marked contrast is provided by the blattoid-orthopteroid orders. There is little doubt that terrestrial mating was established very early in their history, and Alexander (1964) has illustrated the divergences from the primitive mating position. In the simplest (e.g. in Plecoptera and acridoid Orthoptera), the male mounts on the female, grasps her thorax with his fore and mid legs, curls the end of his abdomen under hers, and applies his genitalia to hers in the same relationship as in the original male-beneath position (Fig. 1.27A). Contact can be maintained by general muscular action, and position by the peg-like action of his phallic organs in her genital chamber. The other principal modification may be illustrated by the Blattodea (Fig. 1.27B). The male attracts the female on to his back by means of a dorsal gland (or other tergal structures), joins his genitalia to hers, and the insects then rotate until they point in opposite directions without twisting the terminalia.

The mechanical requirements are entirely different from those of the Ephemeroptera. Strong abdominal claspers are not needed, and would be an impediment to the kinds of rotation that occur in these orders. Small gonocoxites are preserved in Grylloblattodea (Fig. 1.28A), but in the other orders they are absorbed into sternum 9 (S9), which becomes a *subgenital plate* underlying a large genital cavity. Their styles remain recognisable only in Grylloblattodea, Blattodea, Mantodea, some Isoptera and some ensiferan Orthoptera. On the other hand, the phallic organs rising from the base of the genital chamber are often strongly and variously developed. Primitively, there appear to be three, a median penis or penile lobe and a *phallomere* (Figs 1.28A, B) on each side of it; but there is great variation, the penis sometimes acquiring additional sclerotisations, as in Acridoidea, and the phallomeres becoming modified in a variety of ways (Snodgrass 1937). Thus, in Blattodea (Fig. 19.3c) there is gross

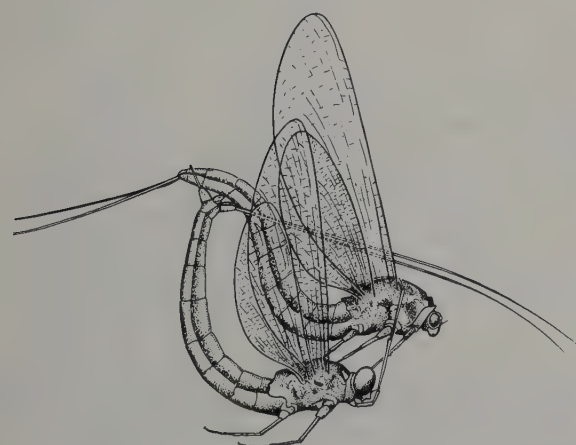


Fig. 1.26 Aerial mating of Ephemeroptera [After Brinck 1957; T. Nolan]

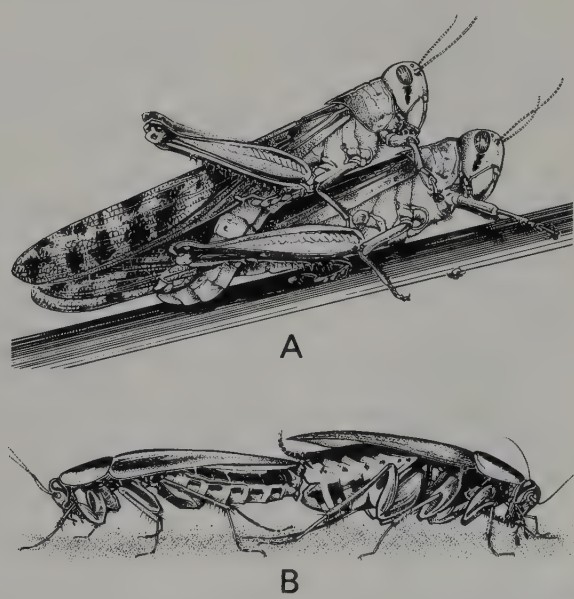


Fig. 1.27 Terminal mating of: A, a locust (ORTH) (after Lecomte 1964); B, *Blattella germanica* (BLAT) (after Roth and Willis 1954). [T. Nolan]

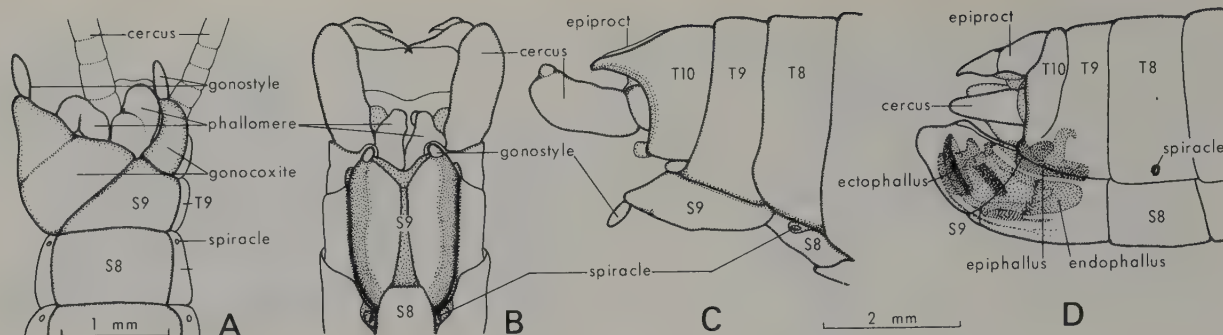


Fig. 1.28 Male terminalia: A, *Grylloblatta campodeiformis* (GRYL), ventral (asymmetrical coxites and styles present); B, *Euconocephalus* sp. (ORTH), posteroventral (coxites absorbed into S9, styles present); C, same, lateral; D, *Gastrimargus musicus* (ORTH), cleared specimen with phallic complex seen through cuticle (S9 divided transversely, but coxites and styles absent).

asymmetry, the penis is replaced by a 'ventral phallomere', and the apex of the left or right phallomere is developed into a strong process, which hooks under the edge of the subgenital plate of the female and retains a hold while the bodies move round. Conversely, in some Plecoptera (which do not rotate) the phallic parts are reduced, and the whole genital chamber may be eversible, or a secondary intromittent organ may be developed from the epiproct (Brinck 1956). The Dermaptera have an elongate, sometimes double penis, but no phallomeres.

So far, the picture is reasonably clear, and it is now necessary to examine two important questions before proceeding further. These concern the composition of the intromittent organs and the homologies of the clasping organs in hemipteroid and endopterygote insects.

The intromittent organ of most higher insects is a more complex structure than the simple penis of apterygotes or Ephemeroptera. It develops postembryonically by fusion of initially paired primary genital papillae to form a median, tubular, often eversible *endophallus* (Snodgrass 1957), with the conjoined ejaculatory ducts opening by the gonopore at its base, and itself opening distally by a *phallotreme* (Fig. 1.29A). Its external walls may become sclerotised or modified in a wide variety of ways. The whole organ is commonly known as the *aedeagus*, and its functions are not always exclusively intromittent. It develops from the tissues behind S9, and some authors regard it as belonging to segment 9, whereas others (e.g. Snodgrass 1957) consider that it is derived from 10. There is even wider difference of opinion on the origins of its sclerites, and especially on the nature of a pair of processes (sometimes called 'parameres' or 'penis valves') that may be present at its sides or incorporated in its lateral walls (Fig. 1.29B). They may not be homologous with the 'parameres' discussed below, and *parandrite* (Crampton 1938) is probably the best term to use for them when they are present.

The clasping organs of the higher insects generally have been regarded as homologous with the gonocoxites and gonostyles of Ephemeroptera, their reduction in some groups being parallel to what occurs in the blattoid-orthopteroid orders. This theory is based primarily on the comparative anatomy of the adults. It carries the implica-

tion that these appendages are 9th-segment structures, and the suggestion that the ancestors of these insects may have mated in the air, as Ephemeroptera do today. Moreover, strong external clasping would preclude the kind of rotation that is possible in the blattoid-orthopteroid orders, so that deviations from the primitive mating position would be likely to produce twisting of the terminal segments, a phenomenon that is not uncommon in endopterygotes.

On the other hand, Crampton (1938) and Snodgrass (1957) have maintained that these organs are derived from the phallic complex and not the clasping complex of primitive insects, because they arise by subdivision of the primary genital papilla on each side. As the term 'paramere' was first used for the structures in beetles that they believe to be homologous with the clasping organs

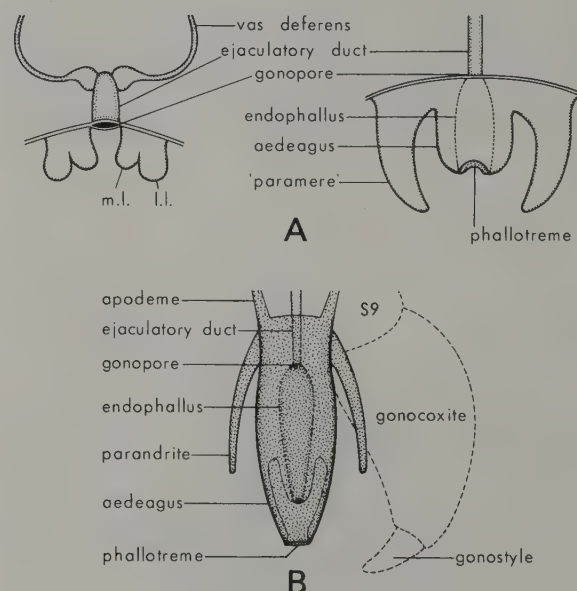


Fig. 1.29 A, development of the external genitalia of the male: left, division of primary genital papillae into medial and lateral lobes (m.l., l.l.); right, fusion of the medial lobes to form the intromittent organ. B, structure of a generalised aedeagus with a pair of parandrites ('parameres').

[After Snodgrass 1957]

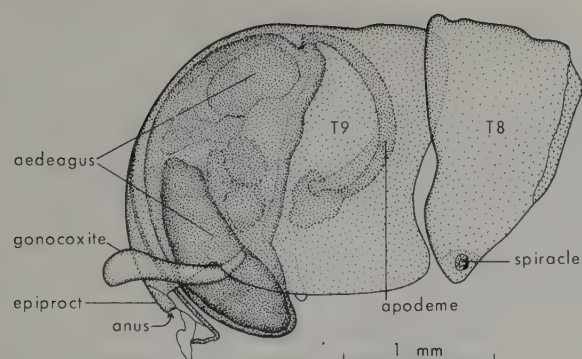


Fig. 1.30 Male terminalia of *Pristhesancus plagipennis* (HEMI), cleared preparation with aedeagus seen through cuticle of pygofer (T9).

of other endopterygotes, they applied it to all. It follows from this theory that the 'parameres' may be 10th-segment structures; that the ancestors of both hemipteroid and endopterygote insects mated on the ground or vegetation, and had already lost all trace of the 9th-segment coxites and styles; and that unsegmented 'parameres' close to the aedeagus (as in beetles; Fig. 1.31C) represent the primitive condition, their development into efficient, two-segmented claspers in the panorpoid orders being a response to increasing mobility of the insects and exposure to hazards during mating.

If hemipteroids and endopterygotes did not evolve from the same ancestral stock, neither theory need be true for both groups. There is some collateral evidence to support the paramere theory in the hemipteroids, but the

weight of probability still lies with the gonocoxite theory for the endopterygotes, and it would seem undesirable to depart from it for either group without further evidence.

End-to-end mating without torsion of the parts seems to be common in the hemipteroid orders, and the genitalia are usually narrow, with approximation of the gonocoxites to the aedeagus and loss of the gonostyle (Fig. 1.30). There is often asymmetry, and in cimicoid bugs this is associated with development of one gonocoxite into a piercing organ for use in haemocoelic insemination (see Hinton 1964). Methods of mating are more varied in the endopterygotes, including primitive side-by-side orientation, as well as male-above, end-to-end and even venter-to-venter in a few Diptera and Hymenoptera. Permanent torsion of the terminal segments is common in Diptera and occasional in other orders. There is a trend towards displacement and reduction of parts in Megaloptera, Neuroptera and Coleoptera, and to loss of styles but development of parandrites on the aedeagus and accessory appendages ('volsellae' or 'claspettes') on the coxites in Hymenoptera (Fig. 1.31B). The panorpoid orders show the greatest variation, from diagrammatic simplicity in some generalised Diptera to complicated arrangements involving, not only the presence of parandrites and claspettes, but various displacements, and the development of a wide variety of accessory lobes or processes, as seen in the Lepidoptera (Chapter 41). There may also be strong apodemes extending into the body from the base of the endophallus, aedeagus or coxites.

Segments 10 and 11 and the cerci are often reduced or partly absorbed, but the appearance of the cerci and paraprocts usually remains characteristic, and is often a valuable aid in orientation when rotation is suspected.

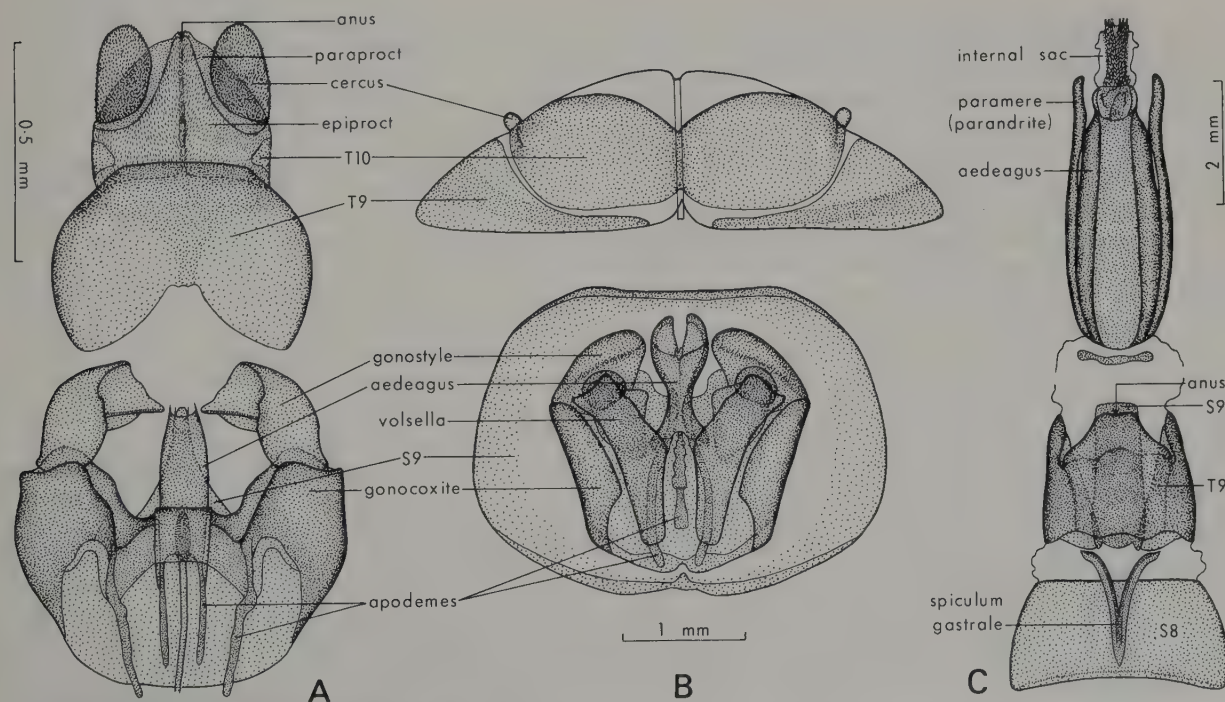


Fig. 1.31 Male terminalia of some endopterygotes (dissected): A, *Chiomyza* sp. (DIPT); B, *Perga affinis* (HYMN); C, *Ptomaphila lacrymosa* (COLE) with T8 removed and aedeagus withdrawn from its resting position within segments 8 and 9.

KEY TO HEXAPOD ORDERS AND SOME OTHER ARTHROPOD GROUPS

by J. F. LAWRENCE

The following is a diagnostic key to the immature and adult stages of all hexapod orders and to some other terrestrial arthropods with which they may be confused. It is based in part on keys found in general texts, such as Brues *et al.* (1954), Borror *et al.* (1976), and Daly *et al.* (1978), and particularly on that included in Stehr (1987a). Illustrations of the various hexapod orders may be found in the taxonomic chapters of this book, but for other arthropod groups the reader should consult the texts mentioned above, as well as Krantz (1978), Snodgrass (1952) and sections in Parker (1982).

1. With 1 or 2 pairs of well-developed wings 2
 - Wingless, or with rudimentary or vestigial wings not suitable for flight 34
- 2(1). Fore wings hard or leathery, at least at base (Figs 23.1; 30.70–73; 35.46), differing in texture from membranous hind wings, which may be absent; prothorax large and not fused with mesothorax, except in Strepsiptera (Fig. 36.8), which have minute fore wings 3
 - Wings membranous (sometimes covered with scales); fore wings similar in texture to hind wings, if present, and never vestigial (Figs 42.1A, B) 11
- 3(2). Fore wings (tegmina or hemelytra) almost always with branching veins (Figs 19.2; 20.2; 24.1; 30.70–73) or if veins absent, hind wings never with transverse folds; head usually hypognathous (Figs 19.1; 24.2) or opisthognathous (Figs 30.1); mouth-parts sometimes haustellate (with sucking tube or proboscis containing stylets, Figs 30.1, 2), without maxillary or labial palps 4
 - Fore wings (elytra) without veins (Figs 23.1; 35.33A) (sometimes with parallel striae which may join apically, Figs 35.2A, E; 35.38A, E); hind wings almost always with transverse, as well as longitudinal folds (Figs 23.2; 35.5B, E), and concealed at rest beneath elytra; head usually prognathous (Figs 23.1; 35.3A); mouth-parts almost always mandibulate, with paired mandibles moving in horizontal plane (Figs 1.4; 35.1); rarely with tubular proboscis containing stylets (Fig. 35.48L), but if so, maxillary and labial palps also present 10
- 4(3). Mouth-parts haustellate, consisting of a slender, tubular proboscis extending below head (Fig. 30.1); maxillary and labial palps absent (adult bugs) **Hemiptera**
 - Mouth-parts mandibulate, with paired mandibles moving in horizontal plane (Figs 1.4; 20.10A, B) 5
- 5(4). Hind wings not folded, similar in structure to fore wings (Figs 20.1A; 20.3); fore wing with sclerotised portion very short and separated by line of weakness which allows wing to be shed (Fig. 20.2A) (winged reproductive termites) **Isoptera**
 - Hind wings broader than fore wings, and capable of being folded longitudinally in a fan-like manner (Figs 24.1; 36.8) 6
- 6(5). Small to minute species (less than 5 mm long); antennae short, 4- to 7-segmented, with at least one segment flabellate (with a long, flat lateral process); fore wings minute; prothorax reduced; cerci absent (Fig. 36.8) (adult male strepsipterans) **Strepsiptera**
 - Larger species (rarely less than 5 mm long); antennae longer, almost always with more than 7 segments and never flabellate; fore wings rarely minute; prothorax large and free from mesothorax; cerci present 7
- 7(6). Hind legs almost always modified for jumping (Figs 24.2, 14), their femora usually thickened and their femora and tibiae noticeably longer than those of mid leg (when mid and hind legs similar, then body cylindrical or laterally compressed and fore legs modified for digging, Fig. 24.16C); pronotum with large, descending lateral lobes (Figs 1.2; 24.2); abdominal tergites distinctly larger than sternites; usually capable of producing sound by stridulation (adult grasshoppers, katydids, crickets etc.) **Orthoptera**
 - Hind legs not modified for jumping; if somewhat larger than mid legs, then without thickened femur or with both femur and tibia laterally expanded and leaf-like (Fig. 25.7, 10); if fore legs modified for digging, then body oval and flattened; pronotum without large, descending lateral lobes; incapable of stridulation 8
- 8(7). Body oval and flattened; head strongly hypognathous and almost or quite concealed beneath prothorax; legs similar in form and more or less equal in size, with large, narrowly separated coxae and spinose tibiae (Figs 19.2B, 8) (adult cockroaches) **Blattodea**
 - Body elongate and usually narrow; head not concealed beneath prothorax; coxae smaller (Fig. 25.11) or fore legs raptorial (Figs 21.5–10) 9
- 9(8). Prothorax much longer than mesothorax; fore legs raptorial, adapted for grasping prey; coxae very large; cerci usually with several segments (Figs 21.5–10) (adult mantids) **Mantodea**
 - Prothorax shorter than mesothorax; fore legs not raptorial; coxae small and well separated; cerci 1-segmented (Figs 25.2, 6) (adult stick and leaf insects) **Phasmatodea**
- 10(3). Abdominal apex with large, strongly sclerotised, articulated, forceps-like cerci (Fig. 23.1); antennae long and slender, multisegmented; elytra short, leaving most of abdomen exposed; hind wings almost circular, with fan-like, radial folds (Fig. 23.2) (adult earwigs) **Dermaptera**
 - Cerci absent (if forceps present at abdominal apex, then elytra concealing most of abdomen); antennae usually shorter, with less than 12 segments, or with segments flabellate; hind wings (Fig. 35.5) not circular and folding not radial (adult beetles) **Coleoptera**
- 11(2). With 1 pair of wings (on mesothorax) (metathoracic wings sometimes represented by minute halteres) 12
 - With 2 pairs of wings 17

- 12(11). Abdominal apex with 1–3 long filaments (Fig. 16.1); mouth-parts vestigial 13
 Abdominal apex without long filaments; mouth-parts almost always well-developed, mandibulate or haustellate 14
- 13(12). Wings with numerous veins and cells (Fig. 16.1A); halteres absent; antennae short and bristle-like (Fig. 16.1B); abdominal apex with 2 or 3 multisegmented appendages (paired cerci and median stylus) (Fig. 16.1) (few adult mayflies) **Ephemeroptera**
 Wings with only 1 or 2 veins; halteres present; antennae long and conspicuous; abdominal apex with a single caudal stylus or brush(es) of waxy filaments (Fig. 30.25A) (adult male Coccoidea) **Hemiptera**
- 14(12). Halteres present (Figs 39.5A, B); mouth-parts almost always haustellate (Fig. 39.3) or vestigial (if mandibulate, body length less than 1 mm); maxillary palps present; prothorax usually highly reduced and closely adpressed to enlarged mesothorax (Fig. 39.5); tarsi almost always 5-segmented 15
 Halteres absent; mouth-parts mandibulate (Fig. 1.4) or maxillary palps absent (Figs 30.37i, j); prothorax well developed and conspicuous (Figs 28.6c; 30.37k, l, 46); tarsi 2- or 3-segmented 16
- 15(14). Abdomen constricted basally, with a 2-segmented petiole (Fig. 42.25D); wings fringed with long hairs; mouth-parts mandibulate; total length less than 1 mm (adult Mymarommatidae) **Hymenoptera**
 If abdomen constricted basally, petiole undivided; wings not fringed with long hairs; mouth-parts haustellate or occasionally vestigial; total length usually greater than 1 mm (adult flies) **Diptera**
- 16(14). Mouth-parts mandibulate (Fig. 1.4); antennae long and conspicuous (Fig. 28.6), with at least 13 segments; maxillary and labial palps present (adult booklice and barklice) **Psocoptera**
 Mouth-parts haustellate consisting of a slender, tubular proboscis extending below head (Figs 30.37i, j); antennae short and bristle-like, with less than 11 segments (Figs 30.37f, i, j); maxillary and labial palps absent (adults of Peloridiidae and some Fulgoroidea) **Hemiptera**
- 17(11). Wings largely or entirely covered with flattened scales, which may be intermixed with hairs and which usually form a pattern (Figs 41.5, 47, 64); mouth-parts usually consisting of a coiled proboscis (Figs 41.1, 22) (occasionally vestigial or rarely mandibulate) (adult butterflies and moths) **Lepidoptera**
 Wings without scales; mouth-parts not forming coiled proboscis 18
- 18(17). Wings long and very narrow, with 2 veins or less, and fringed with long hairs (Fig. 31.5); tarsi 1- or 2-segmented with pretarsal arolium forming protrusible bladder (Fig. 31.1c); minute insects, usually less than 5 mm long (adult thrips) **Thysanoptera**
 Wings usually broader and with several to many veins; if wings somewhat linear, then tarsi with more than 2 segments and without bladder-like arolium 19
- 19(18). Fore wings relatively large and hind wings small and rounded; wings at rest held together above body and provided with numerous cross-veins and cells (Fig. 16.1A); antennae short and bristle-like (Fig. 16.1B); abdominal apex with 2 or 3 multisegmented caudal filaments (Fig. 16.2) (adult mayflies) **Ephemeroptera**
 Without above combination of characters 20
- 20(19). Tarsi 5-segmented 21
 Tarsi with 4 segments or fewer 27
- 21(20). Fore wings conspicuously hairy (Figs 40.1, 3); mouth-parts vestigial, except for palps, which are usually well-developed and conspicuous (Fig. 40.2c); antennae usually at least as long as body (adult caddis-flies) **Trichoptera**
 Surface of fore wings not hairy or with microscopic hairs only; mandibles well-developed; antennae shorter than body 22
- 22(21). Wings without cells (membrane may have fine reticulations) (Fig. 20.2); abdomen not constricted near base; prothorax large and free from mesothorax (Fig. 20.1A) (winged reproductives of *Mastotermes*) **Isoptera**
 Wings almost always with at least 1 cell (Figs 34.1; 37.1; 42.9), or if cells absent, then abdomen constricted near base (between propodeum and metasoma) and prothorax reduced and closely adpressed to mesothorax (Figs 42.1A, B, 8) 23
- 23(22). Fore wings and hind wings markedly different in shape and venation, the former about 1.5 times as long as the latter (Fig. 42.8); fore wings with less than 20 cells; abdomen often constricted at base; prothorax reduced and closely adpressed to mesothorax (Fig. 42.6) (adult bees, wasps, sawflies etc.) **Hymenoptera**
 Fore wings about the same length as hind wings and usually similar in shape and venation (Figs 34.1; 37.1); fore wings with more than 20 cells; abdomen not constricted at base; prothorax larger and more or less free from mesothorax 24
- 24(23). Costal area of fore wing without cross-veins; head more or less produced forming a rostrum (Figs 37.2, 9, 10) (adult scorpion-flies) **Mecoptera**
 Costal area of fore wing with 2 to many cross-veins; head without a rostrum (Figs 32.1; 33.1; 34.3) 25
- 25(24). Prothorax elongate and more or less cylindrical; head elongate; fore legs not enlarged and raptorial (Fig. 33.1). Not occurring in Australia (adult snake-flies) **Raphidioptera**
 Prothorax rarely elongate; if so, then fore legs enlarged and raptorial (adapted for grasping prey, Fig. 34.3D) 26
- 26(25). Hind wings considerably broader at base than fore wings (Fig. 32.1); wing veins not bifurcating near wing margin; relatively large insects with forewing 8 mm or more in length (adult alderflies and dobsonflies) **Megaloptera**
 Hind wings as broad as or narrower than fore wings (Figs 34.1, 7, 8), with veins almost always bifurcating near wing margin (except in minute species of Coniopterygidae, Fig. 34.9A, in which fore wing is shorter than 5 mm and covered with wax-like powder) (adult lacewings, owl-flies, antlions etc.) **Neuroptera**

- 27(20). Mouth-parts haustellate, consisting of a slender, tubular proboscis extending below head (Figs 30.1, 18, 371, J); maxillary and labial palps absent (adult aphids, cicadas, leafhoppers etc.) **Hemiptera**
 Mouth-parts mandibulate, consisting of opposable mandibles which move in a transverse plane (Figs 17.2; 18.1c); maxillary and labial palps present 28
- 28(27). Wings with numerous cross-veins and cells 29
 Wings without numerous cross-veins and cells 30
- 29(28). Antennae minute and bristle-like, with less than 6 segments; cerci 1-segmented (adult dragonflies and damselflies) **Odonata**
 Antennae long and conspicuous, multisegmented; cerci usually multisegmented (adult stoneflies) **Plecoptera**
- 30(28). Body usually with strong constriction near base of abdomen (between propodeum and metasoma) (Fig 42.25); head with very narrow neck; fore wings with 1 or 2 veins and hind wings with 1 vein or none (Fig. 42.25); antennae with scape much longer than pedicel and the joint between them forming an angle (elbowed) (Fig. 42.25) (adults of some Chalcidoidea) **Hymenoptera**
 Base of abdomen never constricted; neck much broader; fore wings with more than 2 veins and hind wings usually with more than 1 vein; antennae not elbowed 31
- 31(30). Fore legs with basal tarsal segment enlarged and distended, forming silk-producing organ (Fig. 26.1A) (adult embiids or web-spinners) **Embioptera**
 Fore legs with tarsal segments about equal 32
- 32(31). Tarsi with 4 segments; wings more or less equal in length (Fig. 20.1A) (winged reproductive termites) **Isoptera**
 Tarsi with 2 or 3 segments; hind wings shorter than fore wings (Figs 27.2; 28.2) 33
- 33(32). Cerci absent; antennae filiform, with more than 13 segments (Fig. 28.1A); wings with at least 4 longitudinal veins and usually with several enclosed cells (Fig. 28.2) (adult booklice and barklice) **Psocoptera**
 Cerci present; antennae moniliform and 9-segmented (Fig. 27.1); fore wing with 3 main longitudinal veins and no cells (Fig. 27.2). Not yet recorded from Australia (adult zorapterans) **Zoraptera**
- 34(1). With 3 or fewer pairs of thoracic legs (or walking legs when thorax and abdomen are not differentiated) 35
 With 4 or more pairs of legs 112
- 35(34). Thorax or first 3 trunk segments with 2 or 3 pairs of legs, which are usually segmented with terminal claws, but may be minute or reduced to conical, unsegmented protuberances 36
 Thorax without legs, with 1 small pair, or occasionally with a single median proleg (Fig. 39.13E) 69
- 36(35). Antennae branched; body apparently 4-segmented, each segment bearing a dorsal plate; segment 1 with 1 pair of legs and segment 2 with 2 pairs (first instar pauropods) **Pauropoda**
 Antennae unbranched or absent; without other characters in combination 37
- 37(36). Head not evident (reduced to capitulum); body segmentation rarely evident; antennae absent; abdomen fused to rest of body, which is compact and usually ovoid; size minute (first instar and few adult ticks and mites) **Acarina**
 Head and body segmentation almost always evident (not so in some Coccoidea, which have a long proboscis extending posteriorly from beneath head region); antennae almost always present 38
- 38(37). Segmented legs on 2nd, 3rd and 4th segments behind head; first trunk segment (collum) legless (first instar millipedes) **Diplopoda**
 Segmented legs on first 2 or 3 segments behind head; first segment always with legs 39
- 39(38). Antennae absent; fore legs held forward like antennae (Fig. 12.1A); abdomen with paired ventral appendages on first 3 segments; size usually less than 1.5 mm (adult and immature proturans) **Protura**
 Antennae present (sometimes greatly reduced); fore legs usually used for walking, sometimes reduced; abdomen with ventral appendages absent, or not confined to first 3 segments, or not on all 3 of them; size usually greater than 1.5 mm 40
- 40(39). Abdomen with ventral tube (collophore) on segment 1 and usually with a forked jumping organ (furcula) on segment 4 (Fig. 11.1A); number of abdominal segments 6; size usually less than 6 mm (adult and immature springtails) **Collembola**
 Collophore and furcula absent; abdomen with more than 6 segments 41
- 41(40). Abdomen with paired ventral styli on 2 or more of abdominal segments 1–9 (Figs 13.2–3; 14.1F–H; 15.1F, G); abdominal apex with pair of forceps (Figs 13.3A, D) or 2 or 3 filamentous appendages (Figs 13.3B; 14.2; 15.2) 42
 Abdomen without ventral styli, sometimes with ventral prolegs (Figs 35.18G; 37.7E, H; 41.71) or gills (Fig. 34.10D), or occasionally with a posterior pair of stylus-like appendages (Figs 35.13D; 36.5) 44
- 42(41). Abdomen with 2 terminal appendages that may be filamentous or forceps-like (Fig. 13.3); ventral styli on segments 1–7 or 2–7; tarsi 1-segmented; compound eyes absent; body without scales (adult and immature diplurans) **Diplura**
 Abdomen with 3 terminal filamentous appendages (Figs 14.2; 15.2); ventral styli on segments 2–9, 7–9 or 8–9; tarsi 2- to 4-segmented; compound eyes usually present; body scaly 43
- 43(42). Body somewhat cylindrical; thorax strongly arched; compound eyes large and usually touching (Fig. 14.2) (adult and immature bristletails) **Archaeognatha**
 Body flattened; thorax not arched; compound eyes small and widely separated, or absent (Fig. 15.2) 44

- (adult and immature silverfish) **Thysanura**
- 44(41). Ectoparasites of birds, mammals or honeybees and usually found on hosts; body leathery and either laterally compressed (Fig. 38.1) or dorsoventrally flattened (Figs 29.1; 30.58A; 39.39B) 45
Not ectoparasites of birds, mammals or honeybees (phoretic instars or triungulins, Figs 35.53c; 36.5, may be found attached to the hairs of bees); body usually not as above 48
- 45(44). Tarsi 5-segmented; antennae short and usually concealed in grooves (Figs 38.6; 39.39B) 46
Tarsi 1- or 3-segmented 47
- 46(45). Body laterally compressed; legs extending ventrally; usually capable of jumping (Fig. 38.1A)
..... (adult fleas) **Siphonaptera**
Body dorsoventrally flattened; legs extending laterally; not capable of jumping (Fig. 39.39B)
..... (adult Braulidae, Hippoboscidae and Nycteribiidae) **Diptera**
- 47(45). Tarsi 3-segmented; antennae longer than head (Fig. 30.58A)
..... (adult and immature Cimicidae and Polycetenidae) **Hemiptera**
Tarsi 1-segmented; antennae shorter than head (Fig. 29.1) (adult and immature lice) **Phthiraptera**
- 48(44). Compound eyes absent; wing pads absent; tarsi 1-segmented or absent; 1 to 7 simple larval eyes (stemmata) often present laterally (occasionally up to 30 grouped together forming 'pseudocompound' eyes, Figs 37.7B, G, I) 49
Compound eyes present (Figs 16.12; 17.9; 18.3) (sometimes reduced or secondarily absent); wing pads often present (Figs 16.12, 14; 17.9, 10; 18.6); tarsi usually 2- to 5-segmented (1-segmented in some Ephemeroptera, Thysanoptera and Hemiptera; absent in some immature Thysanoptera and Hemiptera); stemmata absent but 1 to 3 simple adult eyes (ocelli, Fig. 1.4) may be present dorsally in addition to compound eyes 91
- 49(48). Mouth-parts haustellate, with stylets arising from rear of head (Figs 30.16E-G); maxillary and labial palps absent; on plants (some Coccoidea) **Hemiptera**
Mouth-parts mandibulate (Figs 1.4, 7; 41.10A-C) (rarely reduced and non-functional), or if stylet-like, then labial palps present (Fig. 35.16G) 50
- 50(49). Abdomen with 2 or more pairs of soft, unsegmented, fleshy or peg-like prolegs (Figs 37.7E, H; 41.10D-I, 11, 71; 42.13A, C) that may or may not bear rows or rings of hooks (crochets) (prolegs considered to be present whenever groups of crochets occur on ventral surface of abdomen) 51
Abdomen almost always without prolegs or with 1 terminal pair that may bear 1-3 claws or several setae or spines (Figs 35.39D, E; 40.11A, B); some Coleoptera larvae (few aquatic Hydrophilidae and most Oedemeridae) have ventral protuberances (ampullae) which may bear groups of irregularly arranged spinules or asperities (Fig. 35.18G) 54
- 51(50). Pairs of prolegs fewer than 5, usually located on abdominal segments 3-6 and 10 (Fig. 41.71); if prolegs also present on segments 2 and 7, then 2 and 7 without crochets; crochets present, usually hook-like and forming rows or circles (Figs 41.10D-I); head usually with distinct adfrontal areas formed between paired endocarinae and ecdysial lines (Figs 41.10A, C) (most larval Lepidoptera, caterpillars) **Lepidoptera**
Pairs of prolegs 6 or more (Figs 37.7E, H; 42.13A, C); crochets absent, but prolegs may bear 1 or 2 claws; adfrontal areas absent 52
- 52(51). Body with 4 single or double, longitudinal rows of stout setae; size usually less than 5 mm; head retractile; pairs of prolegs on segments 1-8 each bearing a single claw (larval Micropterigidae) **Lepidoptera**
Body without rows of large, stout setae; size usually greater than 5 mm; head rarely retractile; 4-10 (usually 7 or 8) pairs of prolegs, short or long with 1 or 2 claws that may be minute or rarely absent 53
- 53(52). Stemmata 7 or more pairs (up to 30 pairs forming 'pseudocompound' eyes, Figs 37.7B, D, E, G-I); prolegs almost always present on abdominal segment 1; usually 8 pairs (varying from 0 to 8); abdominal segments not transversely subdivided or ringed, often spiny (Figs 37.7E, H); terminal abdominal segment often forming suctorial disc (Fig. 37.7F) (most larval scorpion-flies) **Mecoptera**
Stemmata 1 pair only; prolegs absent on abdominal segment 1; usually 7 or 8 pairs (varying from 6 to 10); abdominal segments usually transversely divided or ringed and rarely spiny (Figs 42.13A-C); suctorial disc absent
..... (most larval sawflies) **Hymenoptera**
- 54(50). Head hypognathous, with mouth-parts directed ventrally (Fig. 41.71) 55
Head prognathous, with mouth-parts directed anteriorly (Figs 32.6; 35.13D) 58
- 55(54). Body ventrally flattened and slug-like (Fig. 41.53B); stemmata usually 6, arranged in semicircle; adfrontal areas present (larvae of Limacodidae) **Lepidoptera**
Body variable, but not slug-like; stemmata not arranged in semicircle; adfrontal areas absent 56
- 56(55). Terminal abdominal segment usually with 1 pair of anal prolegs, each bearing 1-3 hooked claws (Figs 40.11A, B); tarsi with 1 claw; body often with gills and enclosed in a case (Figs 40.12, 15); almost always aquatic (rarely in very damp terrestrial habitats) (caddis-fly larvae) **Trichoptera**
Terminal abdominal segment without prolegs bearing hooked claws; tarsal claws 0-2; body rarely with gills, rarely enclosed in case 57
- 57(56). Stemmata 1 pair; labial palps usually 3-segmented (2-segmented in a few leaf miners); labium usually with distinct salivary opening (spinneret) (Fig. 42.13G), which may be paired; thoracic legs not distinctly elbowed, short and straight; almost always with 2 pairs of thoracic spiracles located on prothorax and mesothorax or in folds between segments (rarely on prothorax alone); body elongate and lightly sclerotised, more or less cylindrical
..... (some larval sawflies) **Hymenoptera**

- Stemmata usually 2–6 pairs or absent, rarely with 1 pair only; spinneret absent; thoracic legs usually elbowed at 1 or more joints; with 1 pair of thoracic spiracles, usually located on mesothorax, but occasionally on prothorax (spiracles occasionally vestigial or replaced by gills) (some beetle larvae) **Coleoptera**
- 58(54). Body with 4 single or double rows of stout setae; size less than 5 mm; head retractile; abdominal segments 1–8 each with a pair of small, ventral claws or hooks (larval Micropterigidae) **Lepidoptera**
- Body without such rows of stout setae; size often greater than 5 mm; head rarely retractile; paired ventral hooks absent 59
- 59(58). Thoracic legs with 2 claws (Figs 32.6; 35.18A) 60
- Thoracic legs with 1 claw or rarely with none (Figs 35.18B–D; 40.12) 64
- 60(59). Labrum and clypeus distinct (Figs 32.4A; 35.19D); terminal abdominal hooks, if present, located on paired prolegs (Fig. 32.4C) 61
- Labrum and/or clypeus absent, or fused so that only one is apparent, or concealed beneath margin of head (Figs 33.5; 35.21i); terminal abdominal hooks, if present, not on paired prolegs 63
- 61(60). Abdomen with 7 or 8 pairs of long lateral processes (Figs 32.6); aquatic (larval dobsonflies and alderflies) **Megaloptera**
- Abdomen without such lateral processes 62
- 62(61). Labial palps 3-segmented; with 4–7 well-developed stemmata; antennae more than half as long as head width; terminal abdominal segment simple (Fig. 33.5). Not occurring in Australia (larval snake-flies) **Raphidioptera**
- Labial palps with 1 or 2 segments; usually without stemmata or with 1 pair only (occasionally with a few small eye spots); antennae short, less than half as long as head width; abdomen usually terminating in a median spine (Fig. 35.19D) (larval Archostemata) **Coleoptera**
- 63(60). Maxillary palps absent; mandibles and maxillae united on each side to form piercing-sucking jaws (Fig. 34.5) (larval lacewings, antlions, etc.) **Neuroptera**
- Maxillary palps present; mandibles and maxillae not united (Figs 35.21, 22G) (most larvae of Adephaga) **Coleoptera**
- 64(59). Mandibles and maxillae modified into long stylets (Fig. 34.10C); gills folded beneath abdomen; antennae with 5 to 16 segments; associated with freshwater sponges (larval Sisyridae) **Neuroptera**
- Mandibles usually opposable, of the chewing type (Figs 1.4, 7; 35.16H–J; 41.10A–C); if mandibles stylet-like, then antennae with 3 segments or less; gills, if present, not folded beneath abdomen; not associated with freshwater sponges 65
- Mandibles absent and maxillae absent or represented by palps only; tarsal claws absent; gills absent; antennae absent or bristle-like (Fig. 36.5); minute (less than 1.5 mm long) (first instar triungulins) **Strepsiptera**
- 65(64). Abdominal apex with a pair of anal prolegs, each bearing 1–3 hooked claws (Figs 40.11, 12); thoracic legs with 6 or occasionally 7 segments, including tarsal claw; spiracles absent; lateral abdominal gills usually present; often larva enclosed within a case formed of silk and debris (Fig. 40.15); habitat aquatic (larval caddis-flies) **Trichoptera**
- Abdominal apex without prolegs bearing hooked claws; thoracic legs almost always with 5 or fewer segments, including tarsal claw (rarely with 6 segments); spiracles almost always present; abdominal gills absent (sometimes with retractile gills in anal region); if living within case, then case composed of faeces and habitat terrestrial 66
- 66(65). Leaf miners 67
- Not mining leaves 68
- 67(66). Labium with protruding spinneret (Figs 41.10A, B); thoracic spiracle on prothorax and not adjacent to mesothorax; adfrontal areas usually evident (Fig. 41.10C) (larvae of various families) **Lepidoptera**
- Labium with protruding spinneret absent (may have median pore); thoracic spiracle on prothorax, rather large and oval and usually very close to mesothorax; metathoracic spiracle very small or vestigial; adfrontal areas absent (some larvae of Tenthredinidae) **Hymenoptera**
- Labium without spinneret or pore; thoracic spiracle on mesothorax only; adfrontal areas absent (some larvae of Chrysomelidae) **Coleoptera**
- 68(66). Number of stemmata on each side about 16, grouped together to form ‘pseudocompound’ eye; thoracic legs with 6 segments, including claw; abdominal apex with paired, ventrally curved hooks and 2 anal papillae (Figs 37.7A–D) (larvae of *Nannochorista*) **Mecoptera**
- Number of stemmata on each side 6 or less, not closely grouped; if thoracic legs with 6 segments, then clypeus and labrum not distinct; abdominal apex without combination of ventrally curved hooks and paired anal papillae (most beetle larvae) **Coleoptera**
- 69(35). Body covered with waxy material, often scale-like in form (Figs 30.16A–D, 21–25); mouth-parts suctorial, arising from rear of head region (Figs 30.16E–G, 21A, 23); sessile and living on plant surfaces (sessile forms of Coccoidea and Aleyrodidae) **Hemiptera**
- Without above combination of characters 70
- 70(69). Head fused with prothorax; body sac-like and unpigmented without distinct segmentation (Figs 36.3, 4); parasitic on other insects, particularly Hymenoptera and Hemiptera; fused head and thorax protruding from between abdominal segments of host (Fig. 36.7) (most adult female strepsipterans) **Strepsiptera**
- Without above combination of characters 71

- 71(70). Mouth-parts and antennae absent or very highly reduced forming unsclerotised lobes; mandibles, if present, completely unsclerotised; resting stages of various hypermetamorphic insects (various families) **Coleoptera, Diptera, Hymenoptera**
- Mouth-parts almost always present; mandibles almost always sclerotised, at least at apex; antennae present (sometimes papillate) 72
- 72(71). Head capsule not distinct, unsclerotised except for mandibles and supporting structures, which may be embedded in prothorax (Fig. 39.10c) 73
- Head capsule distinct, partly or completely sclerotised and usually pigmented (Fig. 35.13); some times partly embedded in prothorax (Figs 35.16A, 39A, 60A) 74
- 73(72). Mandibles opposable, but reduced, varying from pointed mandibles to fleshy, unpigmented structures (Figs 42.13E–J); body often C-shaped and tapering at both ends; thoracic spiracles and abdominal spiracles 5–8 usually inconspicuous; caudal respiratory tube or prothoracic spiracular horn or rake absent; prolegs and crochets absent; usually in cells built by adults or in plant galls; gall-formers never with thoracic rod (spatula) (some larval bees and wasps) **Hymenoptera**
- Mandibles usually parallel, often reduced to 1 or 2 mouth hooks embedded within head (Fig. 39.10c); may be opposable if deeply embedded; if head minute and mandibles difficult to see, then thoracic rod (spatula) often present; body rarely C-shaped, often bearing transverse rows of spinules; spiracles usually on prothorax at or near caudal end, or apparently absent; caudal respiratory tube and/or prothoracic spiracular horn or rake may be present; prolegs sometimes present and may bear crochets; habitat variable, but rarely in cells; gall-formers often with thoracic rod (spatula) (many fly larvae) **Diptera**
- 74(72). Head protracted or only slightly retracted into thorax (Figs 35.13; 39.10A, 13, 14; 41.10A, B, 71; 42.13E) 75
- Head moderately to deeply retracted into thorax; often depigmented and deeply incised posteriorly (Figs 35.16A, 39A, 60A; 39.10B; 41.16A) 88
- 75(74). Thorax and first 2 abdominal segments fused into single mass, to which head is closely adpressed; 5 or 6 apparent abdominal segments separated by deep constrictions, and bearing ventral, median adhesive discs (Fig. 39.14A). Occurring in running water (larvae of Blephariceridae) **Diptera**
- Without above combination of characters 76
- 76(75). Mandibles non-opposable, blade-like or styliform and parallel, or with laterally directed apices (Figs 35.16B; 39.10B) 77
- Mandibles opposable, their apices moving in a transverse plane and capable of meeting one another at midline (Figs 35.16A–J) 78
- 77(76). Mandibles flattened and subtriangular and moving in a transverse plane or highly reduced and fused to head capsule; prothorax greatly enlarged, much wider than abdomen, or head forming a flattened, heavily sclerotised, wedge-like plate which is serrate along anterior edge (Fig. 35.16B); thoracic spiracles on mesothorax and posterior abdominal spiracles not enlarged and laterally placed (larval Eucnemidae) **Coleoptera**
- Mandibles blade-like or styliform and moving vertically or longitudinally (Fig. 39.10B); prothorax not greatly enlarged and head not forming wedge-like plate; thoracic spiracles on prothorax and posterior abdominal spiracles usually enlarged and dorsally or posteriorly placed (Fig. 39.14C) (larvae of Orthorrhapha) **Diptera**
- 78(76). Ventral prolegs present 81
- Ventral prolegs absent 81
- 79(78). Prolegs present on segments 3–6 and 10 (sometimes reduced to crochets arising directly from ventral body wall); head with pair of diverging adfrontal ridges or endocarinae and usually with adfrontal areas between these and the paired ecdysial lines (Figs 41.10A, C); labium with protruding spinneret between palps (Figs 41.10A, B) (some moth larvae) **Lepidoptera**
- Prolegs on different segments with or without crochets; adfrontal ridges and adfrontal areas absent; labium without spinneret 80
- 80(79). Prolegs on abdominal segments 1 to 7 or 8 (few weevil larvae) **Coleoptera**
- Prolegs on prothorax and abdominal apex (Figs 39.13D, E) or on abdominal segments 1 and 2 (larvae of some Nematocera) **Diptera**
- 81(78). Head with paired, diverging adfrontal ridges or endocarinae, and usually with adfrontal areas between these and the paired ecdysial lines (Figs 41.10A, C); labium with a protruding spinneret between palps (some moth larvae) **Lepidoptera**
- Head without adfrontal ridges or adfrontal areas; spinneret or salivary pore absent or antennae reduced to a flattened disc 82
- 82(81). Head hypognathous, with mouth-parts directed ventrally (Figs 35.13C; 42.13E–J) 83
- Head prognathous, with mouth-parts directed forward (Figs 38.3B; 39.14) 85
- 83(82). Antennae distinct (sometimes minute) and basally articulated (Fig. 35.16J); mandibles large, stout, heavily sclerotised and movable (Fig. 35.16J); maxillary palps with 2 or more segments (larvae of a few Anobiidae and most Curculionoidea) **Coleoptera**
- Antennae absent or represented by fixed lobes or pale spots (Figs 42.13E–J); mandibles fixed and very lightly sclerotised or movable, relatively small, and sclerotised at apex only (Figs 42.13E–J); maxillary palps absent or 1-segmented 84
- 84(83). Body more heavily sclerotised, yellow to brown in colour, with segments more or less fused to form rigid capsule;

- with 1 pair of thoracic spiracles and with 8th abdominal spiracles smaller than preceding ones (coarctate larvae of Meloidae) **Coleoptera**
- Body very lightly sclerotised, with segments more or less distinct, not forming rigid capsule (Fig. 42.13E); usually with 2 pairs of thoracic spiracles and with 8th abdominal spiracles about as large as preceding ones (all spiracles sometimes reduced or absent) (most larvae of Apocrita) **Hymenoptera**
- 85(82). Maxillary palps well-developed, with 2 or more segments; labial palps present; thoracic spiracle on mesothorax (if absent, then spiracles on abdominal segments 1–7); if terminal abdominal spiracles enlarged and posterodorsally placed, then head with 6 pairs of stemmata (few beetle larvae) **Coleoptera**
- Maxillary palps absent or 1-segmented; labial palps absent; thoracic spiracle on prothorax or on mesothorax and metathorax (if absent, then abdomen with terminal spiracles only or without spiracles) 86
- 86(85). Spiracles usually on mesothorax, metathorax and first 8 abdominal segments, those on segment 8 laterally placed and not enlarged (Fig. 42.13E); mandibles lightly sclerotised except at apex and usually unidentate; labium with 1 or 2 salivary openings, sometimes forming protruding spinnerets (larvae of some Apocrita) **Hymenoptera**
- Spiracles usually on prothorax and abdominal segment 8, on prothorax and segments 1 to 7 or 8, or on segment 8 only; if metathoracic spiracles present, then those on 8 much larger than preceding ones (Fig. 39.14C); mandibles usually well sclerotised with 3 or more apical teeth; labium without salivary opening or spinneret 87
- 87(86). Antennae conspicuous and 2-segmented; minute spiracles present on prothorax and abdominal segments 1 to 8; each body segment with 1 or 2 transverse rows of long setae (Fig. 38.2B); abdominal segment 10 with dorsal comb of setae and paired ventral struts; in bird or mammal nests (flea larvae) **Siphonaptera**
- Without above combination of characters (larvae of most Nematocera) **Diptera**
- 88(74). Mandibles non-opposable, blade-like or styliform and parallel (Fig. 39.10B), or with laterally directed apices (head sometimes very small and mouth-parts difficult to discern in minute larvae which are often pink in colour and tapered at both ends and with a ventral rod-like sclerite (spatula) on thorax, Fig. 39.14H) (larvae of Cecidomyiidae and some Orthorrhapha) **Diptera**
- Mandibles opposable, their apices moving in a transverse plane and capable of meeting one another at midline ... 89
- 89(88). Apex of abdomen enlarged and more or less truncate, bearing enlarged spiracles which are posterodorsally placed; thoracic segments smaller than most abdominal segments; thoracic and anterior abdominal spiracles absent (larvae of Tipulidae) **Diptera**
- Terminal abdominal spiracles laterally placed and not greatly enlarged; thoracic and anterior abdominal segments present 90
- 90(89). Labium with a protruding salivary opening between labial palps; mandibles with at least 4 apical teeth; body short, broad and ventrally curved. In seeds of *Agathis* (larvae of Agathiphagidae) **Lepidoptera**
- Labium without protruding salivary opening; mandibles with 1 or 2 apical teeth (larvae of Buprestidae, various Chrysomeloidea, Curculionoidea) **Coleoptera**
- 91(48). Labium extensible (folded back on itself and held beneath fore legs), often covering face (Figs 17.9–11); usually aquatic, but sometimes occurring in very wet terrestrial habitats (larval dragonflies and damselflies) **Odonata**
- Labium not extensible or folded back on itself 92
- 92(91). Gills almost always present; cerci long and multisegmented (Figs 16.12, 14; 18.3, 6); habitat aquatic 93
- Gills absent (occasionally with rows of gill-like plastron hairs in aquatic forms with haustellate mouth-parts); cerci variable, but short or absent in aquatic forms 94
- 93(92). Tarsal claws 2; tarsi with more than 1 segment; abdominal apex with 2 terminal filaments (Figs 18.3, 6); finger-like gills beneath thorax (may also be on head, legs and abdomen) (larval stoneflies) **Plecoptera**
- Tarsal claws 1; tarsi with 1 segment; abdominal apex usually with 3 (occasionally 2) terminal filaments (Figs 16.12, 14); filamentous, plate-like or feathery gills present placed dorsally or laterally (Fig. 16.12) (larval mayflies) **Ephemeroptera**
- 94(92). Abdomen usually strongly constricted near base (between propodeum and metasoma) (Figs 42.20G, 23D, 29G, 34), or if not, then antennae elbowed, with scape much longer than pedicel and joint between them forming an angle (Fig. 42.23F) (adult ants and wingless wasps) **Hymenoptera**
- Body not strongly constricted between abdomen and thorax; antennae never elbowed 95
- 95(94). Thorax consisting largely of mesothorax, prothorax and metathorax vestigial; halteres (small, club-like structures on posterior portion of thorax, Fig. 39.5) usually present; if halteres absent, head highly mobile, with very narrow neck, tarsi 5-segmented, and antennae much shorter than head width and usually apparently 3-segmented with bristle-like appendage (arista, Fig. 39.1) at apex (wingless or brachypterous adult female moths) **Lepidoptera**
- Prothorax and metathorax usually distinct (if not, then neck broad or absent, tarsi 1- or 2-segmented, and antennae longer than head width); halteres absent 96
- 96(95). Body densely covered with flattened scales and hairs (Figs 41.5, 47, 64); mouth-parts consisting of coiled proboscis with reduced maxillary palps (Figs 41.1, 22), or inconspicuous; antennae long and multisegmented (wingless or brachypterous adult female moths) **Lepidoptera**
- Body not densely covered with scales, and if hairy, only moderately so; mouth-parts never consisting of a coiled proboscis, but may be inconspicuous; antennae variable 97
- 97(96). Mouth-parts haustellate, consisting of a triangular or stylet-like proboscis for piercing and sucking (Figs 30.2, 18, 19), or rarely absent 98
- Mouth-parts mandibulate, consisting of opposable, chewing mandibles (Figs 1.9A; 20.11) 99

- 98(97). Legs ending in protrusible bladder-like arolium, with or without claws (Fig. 31.1C); proboscis conical and unsegmented; maxillary and labial palps present (immature and wingless adult thrips) **Thysanoptera**
 Legs with 2 claws (rarely 1) and without protrusible, bladder-like arolium; proboscis triangular or long and usually segmented, often consisting of 4 stylets enclosed in trough-like labium (Figs 30.2, 18, 19), rarely absent; maxillary and labial palps absent (aphids, nymphal psyllids etc.) **Hemiptera**
- 99(97). Head usually with conspicuous, swollen postclypeus (area in front of and below antennae, Figs 28.6A, B); prothorax usually inconspicuous, smaller than mesothorax or metathorax; tarsi 2- or 3-segmented; cerci absent (immature and wingless adult booklice) **Psocoptera**
 Head without conspicuous swollen area in front of or below antennae; prothorax conspicuous, about equal to or larger than mesothorax (except in Phasmatodea, which are elongate and stick-like with more than 3 tarsal segments and 1-segmented cerci) 100
- 100(99). Tarsi 2-segmented; cerci 1-segmented, prominent and often with apical spine; antennae 9-segmented and moniliform (Fig. 27.1); minute insects, less than 3 mm long. Not yet recorded from Australia (immature and wingless adult zorapterans) **Zoraptera**
 Tarsi usually 3- to 5-segmented (hind tarsi rarely 2-segmented); antennae variable; cerci usually absent or with more than 1 segment (if 1-segmented, then body length greater than 10 mm) 101
- 101(100). Fore tarsi with basal segment large and bulbous (Fig. 26.1B) (immature and adult embiids) **Embioptera**
 Fore tarsi with basal segment not large and bulbous 102
- 102(101). Hind legs almost always modified for jumping (Figs 24.7, 8A, C, 12), their femora usually thickened and their femora and tibiae noticeably longer than those of mid leg (when mid and hind legs similar, then body cylindrical and fore legs modified for digging, Fig. 24.16C); pronotum with large, descending lateral lobes; abdominal tergites distinctly larger than sternites; usually capable of producing sound by stridulation (most immatures and wingless adults) **Orthoptera**
 Hind legs not modified for jumping; if somewhat larger than mid legs, then without thickened femur or with both femur and tibia laterally expanded and leaf-like (Fig. 25.10); if fore legs modified for digging, then body oval and flattened; pronotum without large, descending lateral lobes; incapable of sound production or producing hissing sounds only 103
- 103(102). Head prolonged to form rostrum with mandibles at apex (Fig. 37.9) (wingless adults of *Apteropanorpa*) **Mecoptera**
 Head not prolonged to form rostrum, or if so, with mandibles not at apex 104
- 104(103). Prothorax much longer than mesothorax; fore legs modified for grasping, their coxae large and mobile (Fig. 21.6B) (immature and wingless adult mantids) **Mantodea**
 Prothorax not greatly lengthened; fore legs not modified for grasping 105
- 105(104). Trochanter absent (Fig. 36.2) (adult female Mengenillidae) **Strepsiptera**
 Trochanter always present between coxa and femur 106
- 106(105). Ventral mouth-parts protracted; head capsule closed ventrally forming gular area between base of labium and posterior edge of head (Fig. 35.1B); antennae with 11 segments or fewer; maxillary palps with 4 segments or fewer; clypeus not distinct (adult beetles without or with very short elytra) **Coleoptera**
 Ventral mouth-parts retracted; head capsule open ventrally, so that labium extends to posterior edge of head (Fig. 1.7); antennae often with more than 11 segments (if fewer, clypeus distinct); maxillary palps 5-segmented 107
- 107(106). Cerci with 4 or more segments 108
 Cerci with 1-3 segments 110
- 108(107). Head hypognathous or opisthognathous (Fig. 19.1); pronotum shield-like and rounded in outline, usually covering all or part of head; body dorsoventrally flattened and oval (Figs 19.4C, D, 8A, D) (immature and wingless adult cockroaches) **Blattodea**
 Head prognathous; pronotum not shield-like and not covering head; body cylindrical and more elongate (Figs 20.1; 22.1) 109
- 109(108). Pronotum longer than wide (Fig. 22.1); antennae filiform; cerci long with 8 or 9 segments; abdomen in females with prominent, sword-like ovipositor. Not occurring in Australia (immature and adult grylloblattids) **Grylloblattodea**
 Pronotum not as long as wide (Figs 20.1B, C); antennae moniliform (beadlike); cerci short, with 4 to 8 segments; females with vestigial or no ovipositor (immature and wingless adult termites) **Isoptera**
- 110(107). Prothorax shorter than mesothorax; tarsi 5-segmented; body very long and narrow, stick-like (Figs 25.8B, C); length usually greater than 30 mm (immature and wingless or brachypterous adult phasmids) **Phasmatodea**
 Prothorax as long as or longer than mesothorax; tarsi with 2 to 4 segments; body not stick-like; length rarely as great as 30 mm, and if so, then cerci large and forceps-like 111
- 111(110). Coxae relatively large, projecting and approximated (Fig. 19.1); cerci very small, 1- to 3-segmented and diverging; tarsi 4-segmented; body usually pale or white (Figs 20.1B, C) (immature and wingless adult termites) **Isoptera**
 Coxae smaller, not projecting and well separated (Fig. 1.12B); cerci large, 1-segmented and convergent, becoming forceps-like in later instars; tarsi with 3 (rarely 2) segments; body usually dark brown or black (Fig. 23.9) (immature and wingless adult earwigs) **Dermaptera**
- 112(34). Antennae branched (adult pauropods) **Pauropoda**

- Antennae not branched or absent 113
- 113(112). Antennae absent (other appendages may be used as antennae); with 4 pairs of segmented legs or leg-like appendages (also with chelicerae and pedipalps, the latter sometimes appearing leg-like) **Arachnida**
- Antennae present; with 5 or more pairs of segmented legs 114
- 114(113). With 6 or 7 pairs of walking legs plus 5 pairs of small, flat plates (pleopods) and 1 pair of tail-like, biramous appendages (uropods) (isopods, amphipods, decapods etc.) **Crustacea**
- All (or all but first pair) of appendages walking legs, which are distributed more or less uniformly along body 115
- 115(114). First pair of legs modified as large, short poison fangs (maxillipeds); legs with 1 claw; with 21 or more pairs of legs or with 15 pairs (7 upon hatching) (immature and adult centipedes) **Chilopoda**
- First pair of legs not modified as maxillipeds; legs with 1 or 2 claws; with 4 or more pairs of legs (often more than 30) 116
- 116(115). Body segments fused in pairs, so that segment 3 and succeeding segments each appear to have 2 pairs of legs; legs with 1 claw; adult usually with 13 or more pairs of legs (3 or rarely 4 pairs at hatching); colour rarely white; size commonly greater than 10 mm (immature and adult millipedes) **Diplopoda**
- Body segments not fused in pairs, with only 1 pair of legs per segment (3 or 4 segments lacking legs); legs with 2 claws; adult with 11 or 12 pairs of legs (usually 6 at hatching); colour white; size rarely greater than 10 mm (immature and adult symphylids) **Symphyla**

ACKNOWLEDGMENTS. The authors are particularly grateful to J. Kulaková-Peck for offering advice on appendages and wings and for providing the original drawings on which Figs 1.17 and 1.18 were based. The following individuals have commented on the order key and have been of great assistance in correcting

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General Anatomy and Function

R. F. CHAPMAN

The object of this chapter is to describe the anatomy of the main organs in the insect's body and, briefly, to describe the functions of each part. Inevitably the treatment is superficial. More detailed general accounts of insect structure and function are to be found in Chapman (1982) and Richards and Davies (1977, Vol. 1). Snodgrass (1935) remains the most useful reference for insect morphology in general, while good accounts of the anatomy of each order occur in the *Traité de Zoologie* (Grassé 1949, 1951). Blum (1985) is the most recent general textbook of insect physiology, while comprehensive accounts, often including anatomy, are found in *Comprehensive Insect Physiology, Biochemistry and Pharmacology* (Kerkut and Gilbert 1985).

THE INTEGUMENT

Basic Structure

The outside of all insects is wholly covered by cuticle which is secreted by the epidermis, a single layer of cells. Together, the cuticle and epidermis comprise the integument (Fig. 2.1). The tracheal system and the fore and hind guts, which are formed by invaginations of the epidermis, are also lined by cuticle.

The outermost layer of the cuticle, the epicuticle, is usually only about 1 μm thick. Beneath it is the chitinous cuticle which may be up to 200 μm thick and is composed mainly of chitin and protein. When first laid down the proteins are not linked together and in this undifferentiated state the chitinous cuticle is known as procuticle. Sometimes it remains in this state, but more commonly the proteins in the outer layers become linked together

and insoluble; this part is then called exocuticle and the inner cuticle, which remains undifferentiated, becomes known as the endocuticle.

Running through the procuticle, at right angles to the surface, are narrow pore canals. These form around slender projections of the epidermal cells which, in the early stages of cuticle production, maintain cytoplasmic connections with the outer layers of the cuticle so that chemicals can be added to pre-existing parts. Epicuticular wax filaments diverge to the wax layer of the epicuticle from the tip of each pore canal and the fused filaments continue down the pore canal to the surface of the epidermis. They may be concerned with the transport of lipids to the surface of the cuticle.

Epicuticle

Although the epicuticle is very thin, it is multilayered and performs several important functions. Terminology for describing the different layers of epicuticle is confused and their chemical nature is not known with certainty. The inner epicuticle is thought to consist of tanned lipoproteins; it forms the bulk of the epicuticle. The outer epicuticle, sometimes called cuticulin, is of unknown composition but probably contains tanned protein. It is the first part of the cuticle to be produced at a moult and appears to define the form of the surface patterns and microstructures such as strigils and plastrons. It is believed to limit the extent to which the cuticle can expand, that is, it does not stretch and expansion is therefore limited by the amount of folding.

The outer epicuticle is coated with wax, a complex mixture of hydrocarbons, alcohols and fatty acids. Its

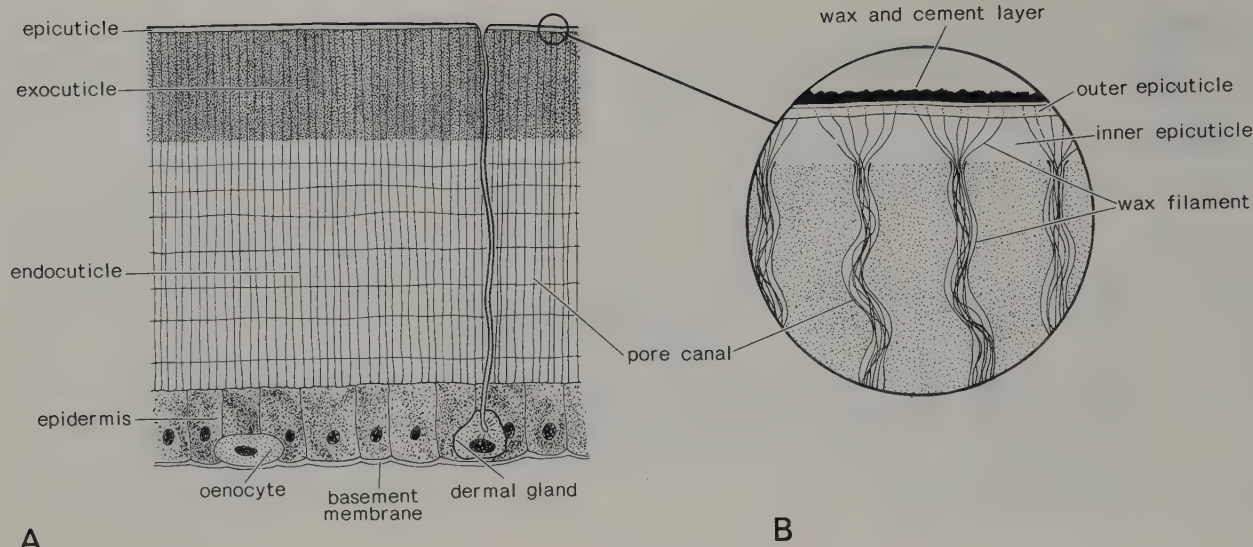


Fig. 2.1 Structure of integument: A, generalised diagram; B, enlargement of outer region.

[After Locke 1961]

composition differs from species to species, but all insect surface waxes so far examined contain *n*-alkanes, generally in the range C_{21} – C_{36} . The wax is the primary waterproofing layer of the insect; its removal or damage with solvents or abrasives, leads to rapid desiccation. There is also an increasing number of examples of components of the wax functioning as sex pheromones, primarily in Diptera, and in caste recognition in termites.

In some insects a layer of 'cement' covers the wax. It is believed to consist of proteins and lipids chemically stabilised by processes similar to tanning (see below); it possibly serves to protect the wax layer.

Chitinous Cuticle

Chitin is a characteristic component of insect cuticle. It is a polysaccharide formed from chains of *N*-acetylglucosamine and glucosamine residues (Fig. 2.2). Molecular chains are held together by physical forces to form microfibrils which are laid down in the plane of the cuticle. The microfibrils formed at one time have a uniform orientation within this plane and the orientation changes progressively with time so that they have a helicoidal arrangement through the thickness of the cuticle. This produces a series of discrete layers (lamellae) distinguished by a 180° rotation of the microfibrils. This is called lamellate cuticle and in most insects the outer pro-

cuticle, which subsequently becomes the exocuticle, is continuously lamellate. The process may continue through the inner layers of procuticle, but sometimes periods of helicoidal deposition of chitin alternate with periods in which the molecular orientation is uniform. The alternation has a circadian periodicity so the resulting growth layers may be used for aging insects (Fig. 2.3). Such layers are present in nymphal and adult Exopterygota and in some adult Endopterygota.

Proteins are the other major constituents of chitinous cuticle and often several different proteins occur in one region of cuticle. No complete structural analysis of an insect cuticular protein has been reported to date, but proteins differing in their overall amino acid composition occur in different types of cuticle.

Proteins give the cuticle its rigidity when they become covalently linked together by *N*-acetyldopamine. This compound is derived from the amino acid tyrosine, and it is partly because of its role in cuticle stabilisation that tyrosine or phenylalanine is an essential dietary constituent for all insects. Insects are unable to manufacture the aromatic ring which is part of the tyrosine molecule. Proteins may become linked to the *N*-acetyldopamine

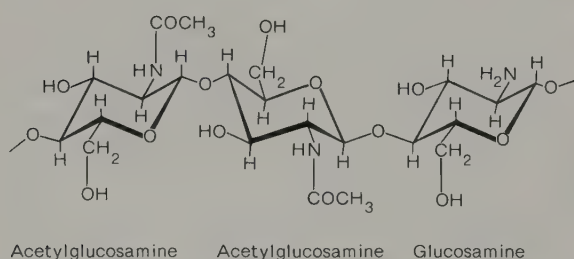


Fig. 2.2 Structure of chitin.

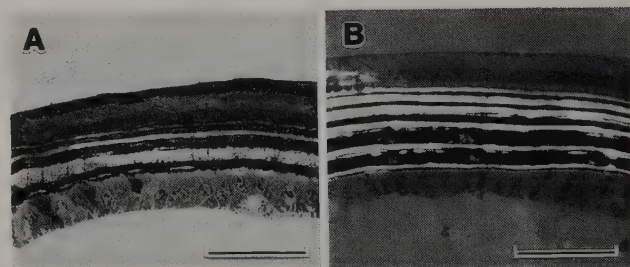


Fig. 2.3 Cuticle growth layers in tibia of *Locusta migratoria* (ORTH: Acrididae) of different ages (transverse sections using polarising microscope): A, specimen killed 3 days after adult emergence, showing 3 pairs of growth layers; B, specimen killed after 6 days, showing 6 pairs of growth layers. Scale = 50 μ m. [C. D. Beaton]

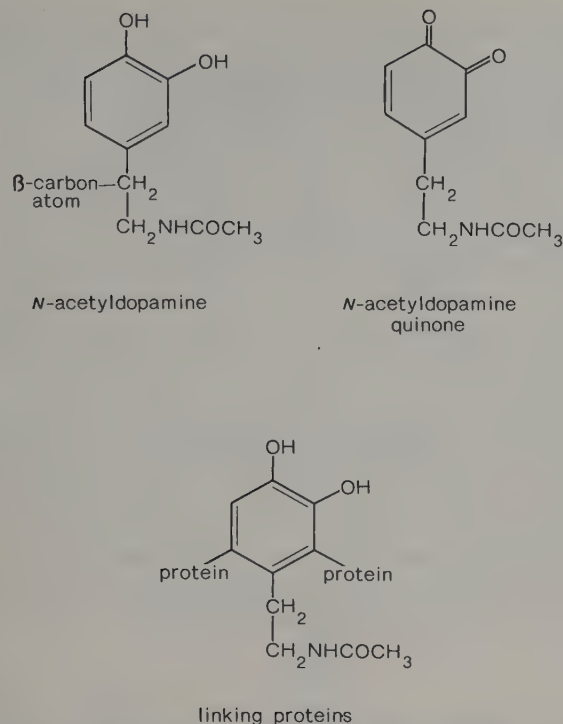


Fig. 2.4 Sclerotisation: diagram showing linking of protein chains by *N*-acetyldopamine.

molecule in two different ways. In quinone tanning, which is most widely accepted as being important, nitrogen atoms in the proteins become directly linked to the aromatic ring of *N*-acetyldopamine (Fig. 2.4). It is also possible that they become linked to the side-chain of the molecule.

The process of stabilisation is called tanning or sclerotisation and hard cuticle is said to be tanned or sclerotised (*not* chitinised). Some degree of dehydration accompanies sclerotisation and this may contribute to cuticular stiffness.

Strength and Flexibility

Sclerotisation hardens the cuticle, but it does not necessarily give it the rigidity to withstand muscular or other forces acting on it. This rigidity can be achieved by an inflection of the cuticle to form an internal ridge orientated along the line of action of the force. Such inflections are visible on the outside of the cuticle as grooves, or sulci (but often incorrectly called sutures). The pleural sulcus is one example (see Fig. 1.11). It indicates the position of the pleural ridge which gives stiffness to the thoracic pleura and prevents distortion by the dorso-ventral flight muscles. Many of the grooves visible in the cuticle have comparable functional significance.

Great strength is achieved by the internal fusion of cuticular inflections. This occurs in the head, where the inflections form the tentorium, and in the thorax, where pleural and sternal inflections (apophyses) often meet (Fig. 2.5).

Flexibility between sclerotised regions is provided by areas of membranous cuticle in which the proteins remain unsclerotised. Sometimes, as between abdominal seg-

ments, there are no points of articulation between the sclerites. Single, monocondylic joints allow for great flexibility of movement, employing a complex musculature. The articulation of the antenna with the head capsule is of this type; so is the insertion of the coxa of Orthoptera where a second articulation, through the trochantin, is not rigid (Fig. 2.6A). Dicondylic articulations only permit movement in one plane and are associated with antagonistic pairs of muscles. The mandibles have dicondylic articulations with the head capsule, and the femoro-tibial articulation is also dicondylic (Fig. 2.6B).

Flexibility associated with elasticity is given by a cuticular protein, resilin, which has rubber-like properties; energy imparted to it when it is distorted is released when the distorting constraints are removed. A pad of pure resilin forms the wing hinge of grasshoppers, storing energy on the upstroke; this energy is used in the downstroke. Resilin also occurs at the base of the hind coxa of fleas, where it provides an energy store for jumping, in the proboscis of Lepidoptera, causing it to coil, and in the labral hinge of Orthoptera, holding the labrum against the mandibles.

Relatively long-term extension of the cuticle sometimes involves plasticisation of membranous areas, permitting them to stretch. This occurs with the abdominal intersegmental membranes of blood-sucking Hemiptera, such as *Rhodnius*, which typically only takes one large meal in each instar during which the abdomen becomes enormously distended. A similar extension of the abdominal intersegmental membranes occurs in grasshoppers during oviposition. These extensions far exceed the increases which can occur by simply unfolding the membranes and involve an increase in hydration. The increase in plasticity is induced by a neurosecretion released from axons terminating at the abdominal epidermis. This is a reversible change, and the membranes slowly return to normal as the abdominal distension subsides.

Cuticular plasticisation also occurs at the time of ecdysis, at least in some insects (see below).

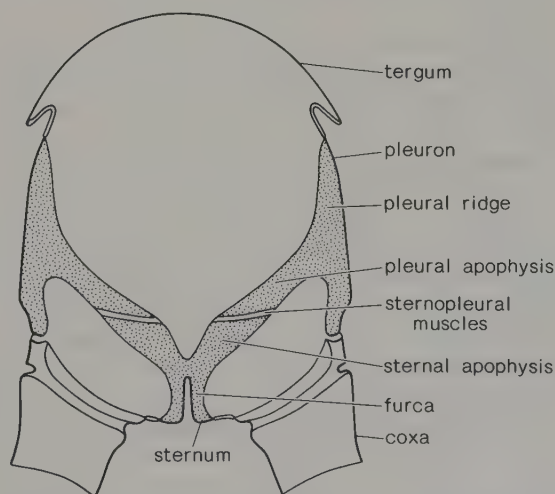


Fig. 2.5 Cuticular strengthening in thorax: transverse section of grasshopper thorax, showing pleural ridge on each side joining sternal apophysis.
[After Snodgrass in Chapman 1982; A. Carter]

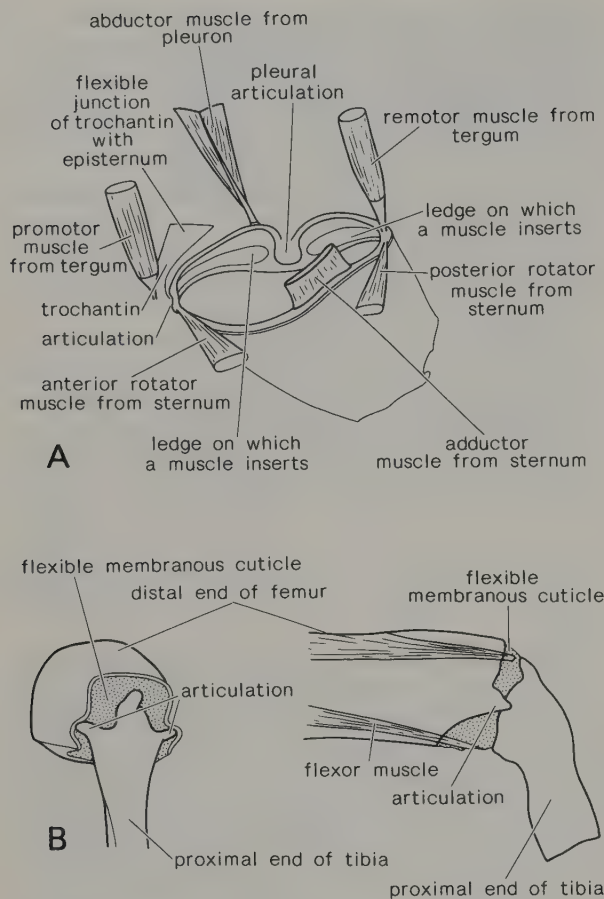


Fig. 2.6 Articulations: A, coxa of grasshopper with single fixed articulation (many muscles involved in regulating movements); B, articulation of tibia and femur (dicondylic articulation with only two muscles). (After Snodgrass in Chapman 1982). [A. Carter]

Growth of the Cuticle

The cuticle limits growth and shedding the cuticle is an essential part of the growth process. The term moulting is usually used to refer to the whole sequence of epidermal and cuticular changes culminating in ecdysis, casting the old cuticle. Moulting is followed by a post-moult period during which the new cuticle expands and is chemically modified. The intermoult then extends to the beginning of the next moult.

Moulting. The first step in the moulting cycle is division of the epidermal cells. Their increase in number is accompanied by a change in form from flattened, often squamous, to columnar. At about the same time, perhaps partly as a result of the changes in cell shape, the epidermis becomes separated from the overlying cuticle. This process of separation is called apolysis. Despite the general separation, muscles retain their connections with the cuticle and sensory receptors remain functional because the nerve dendrites, enclosed in scolopales, extend across the gap between the epidermis and cuticle (Fig. 2.7). Thus the insect can continue to function normally, although apolysis is associated with the beginning of a decline in feeding and general activity which typically occurs towards the end of a larval instar.

Subsequently the epidermal cells secrete moulting fluid into the exuvial space between the cuticle and epidermis. Moulting fluid contains proteolytic and chitinolytic enzymes in an inactive form. Then the cells start to produce the new cuticle, outer epicuticle first and then the new procuticle. The enzymes in the moulting fluid are now activated. They digest unsclerotised parts of the old cuticle, but muscle attachments and nerve connections still remain intact, and the new procuticle is protected by the new epicuticle. The digested remains of the old endocuticle are resorbed and probably provide a reservoir of materials which may be re-used in subsequent cuticle production (Fig. 2.8).

The old cuticle now consists only of a continuous layer of epicuticle with exocuticle remaining wherever it was produced; in some insects an inner layer of endocuticle also resists digestion and persists as a thin membrane, the ecdysial membrane. Casting the cuticle, ecdysis, involves splitting it and then freeing the body from the remains. Usually the insect adopts a particular attitude which facil-

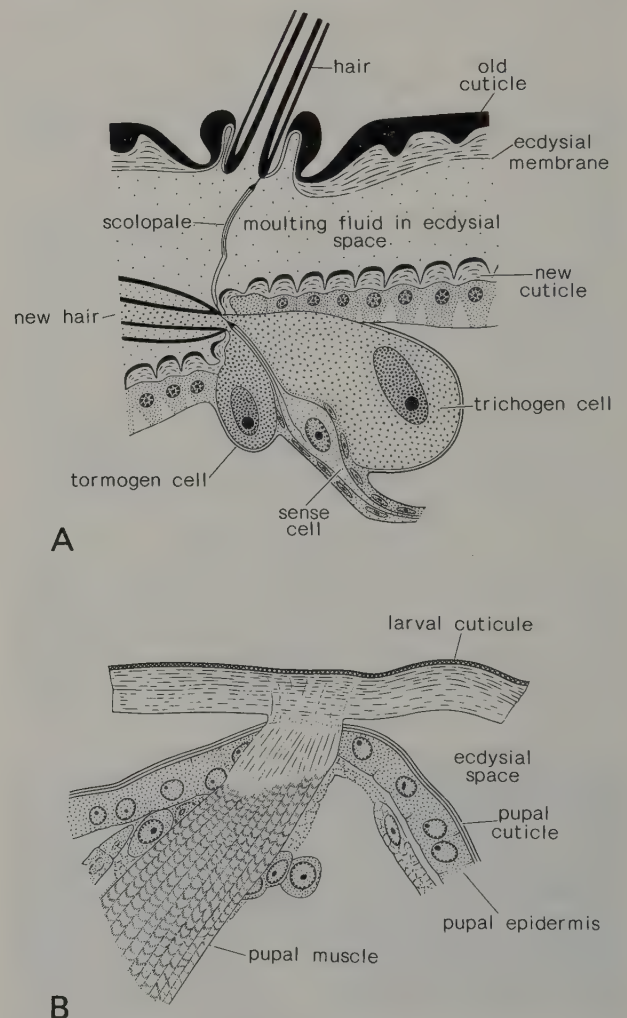


Fig. 2.7 Persistence of muscular and sensory attachments to cuticle after apolysis: A, trichoid receptor showing persistence of scolopale surrounding dendrite across ecdysial space; B, connection of muscle across ecdysial space at larval-pupal moult in *Simulium* (Dipt: Simuliidae).

[From Hinton 1958a, b, by permission of the publishers]

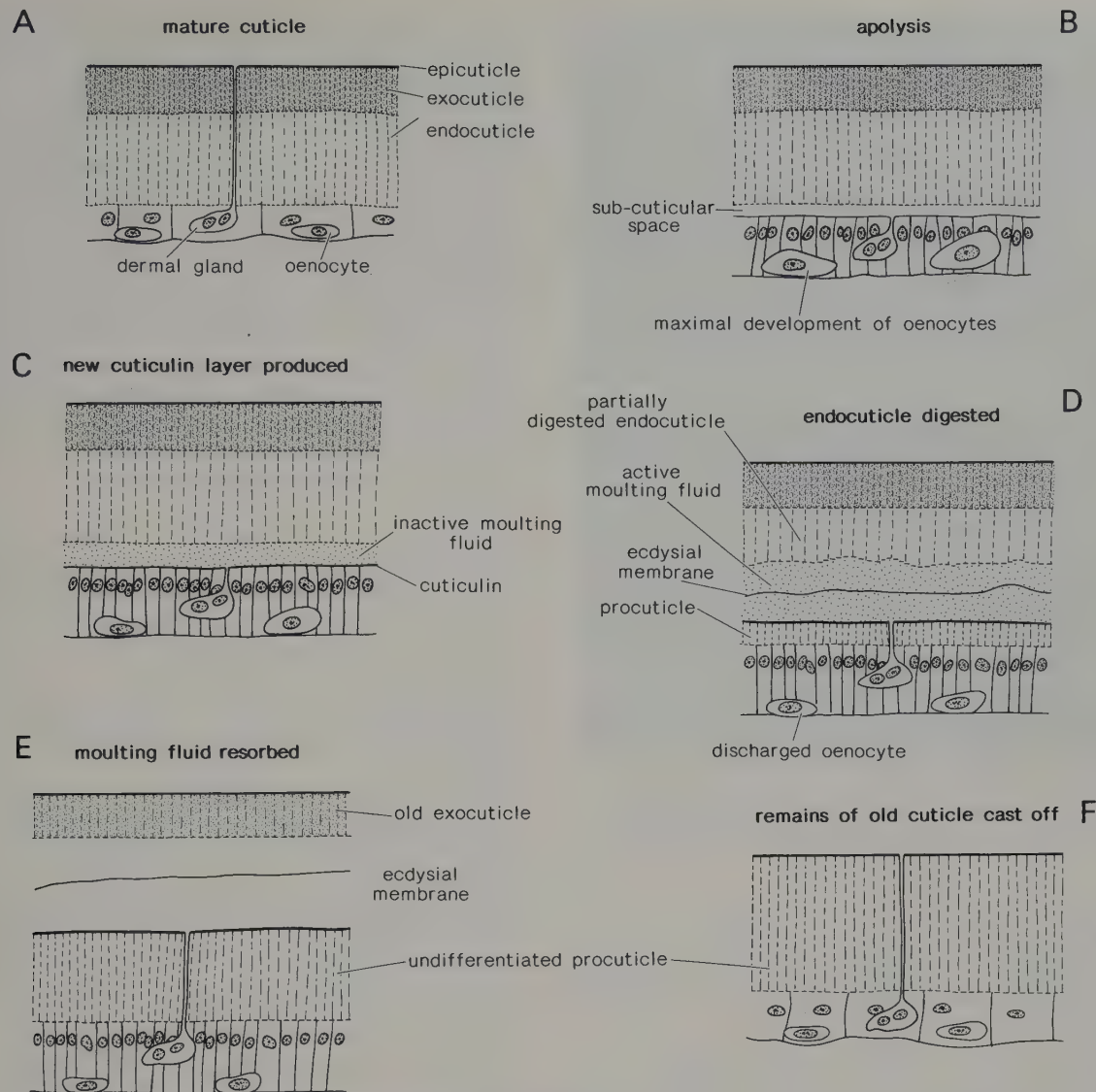


Fig. 2.8 Moult: diagrammatic representation of changes occurring in integument during moult. [After Chapman 1982; A. Carter]

itates escape from the old cuticle before the process starts. An important preliminary to ecdysis is a high blood volume, resulting from the retention of water as the moult approaches. This enables the insect to exert pressure on the old cuticle. Body volume is further enhanced at this time by swallowing air, or water in the case of aquatic insects. Waves of compression passing along the body distend the thoracic region so that it is forced against the old cuticle which is often weakened along a line, the ecdysial line, running along the thorax and on to the head. No exocuticle is present along the ecdysial line so that the pressure causes the cuticle to rupture along it. The insect now pulls itself free of the old cuticle, often aided by gravity. If the old cuticle does not remain attached to the substratum it is often difficult or impossible for the insect to free itself completely. The activity which occurs during ecdysis and the subsequent period of expansion often involves special muscles which are fully developed and functional only at

this time. During the intermoult periods they largely degenerate. They may play an active part in the pumping process, but probably also serve to retain the appropriate spatial relationships between cuticular elements. **Post-moult changes.** Expansion of the new cuticle follows ecdysis by continued pumping of haemolymph forwards and into the appendages. The cuticle is complexly folded and expansion involves the flattening of these folds (Fig. 2.9) while at the same time the procuticle becomes thinner. Expansion of some parts is also facilitated by cuticular plasticisation. The wings of *Manduca*, for example, are relatively inextensible until three or four hours before ecdysis even though the cuticle is still soft. Subsequently the cuticle undergoes two phases of plasticisation during which wing expansion occurs. The expansion is ultimately limited by the inextensible epicuticle. When expansion is complete, the procuticle already laid down (pre-ecdysial cuticle) becomes sclerotised, forming the exocuticle of the newly emerged stage.

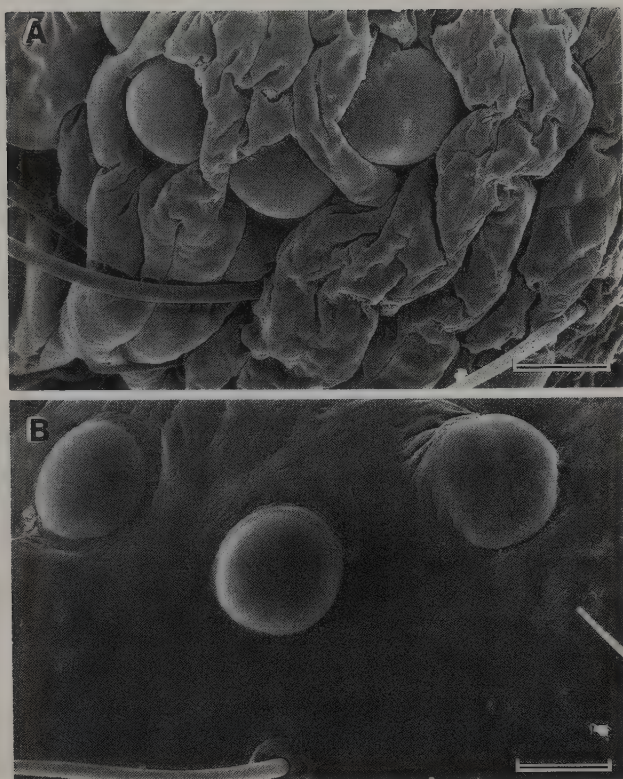


Fig. 2.9 Expansion of cuticle: portion of larval head capsule of *Helicoverpa armigera* (LEPI: Noctuidae) showing stemmata: A, macrofolds and microfolds in pharate insect; B, absence of folding following expansion. Scale = 50 μ m. [C. D. Beaton]

Intermolt changes. Procuticle continues to be laid down throughout the intermolt period in immature insects, and for a limited period in adults. In immature insects this new procuticle remains largely undifferentiated, but in adults it becomes progressively differentiated and only the innermost layers remain unchanged. The biochemical processes are not understood, but it is clear from changes in the staining properties of the cuticle in histological preparations that extensive changes do occur. These changes result in a much harder cuticle, as is often obvious from handling the insects. The lack of differentiation of the intermolt cuticle in larvae enables this material to be re-utilised.

Secretion of wax on to the surface of the cuticle begins shortly before ecdysis and continues through the intermolt period.

Regulation of Cuticular Changes

The factors inducing an insect to moult at a particular time in its development are not known for most insects. In some cases there is evidence that moulting occurs when the insect reaches a particular weight and possibly information on body size is conveyed to the brain by stretch receptors. This is certainly the case in the blood-sucking bug, *Rhodnius*, in which moulting is initiated by stretching of the body wall which results from ingesting a large meal.

Whatever the trigger for moulting, the various process-

es which moulting involves are regulated by hormones. Prothoracicotropic hormone, produced in the median neurosecretory cells of the brain, is released from the corpora cardiaca and stimulates the production of moulting hormone, probably 20-hydroxyecdysone. An increasing titre of the moulting hormone initiates DNA synthesis and division of the epidermal cells; a high titre causes apolysis and starts cuticle production; while a declining titre leads to activation of the moulting fluid and, later, to the degeneration of muscles specifically associated with ecdysis. Ecdysis hormone, released from the central nervous system, causes an increase in cuticle extensibility and releases various patterns of motor activity involved in ecdysis and expansion. It possibly also leads to the release of another hormone from the central nervous system; this hormone, bursicon, contributes to cuticle plasticisation and then initiates tanning.

Colour

Colours are produced by the differential reflection of certain wavelengths of white light. The differential effect (some wavelengths absorbed, others reflected) may be produced by the physical structure of the surface on which the light falls or by the presence, within the surface, of pigments. The colours so produced are known as physical (or structural) and pigmentary colours, respectively.

Physical colours. If light strikes a series of closely spaced, reflecting layers some of the reflected wavelengths may be reinforced while others are cancelled out. The wavelength of the *interference colour* which results depends on the spacing between the reflecting surfaces and on the refractive index of the material. Viewing the surface from different angles is equivalent to changing the distance between successive layers so that the colour observed changes; this is iridescence.

In insects, the lamellae in the cuticle produced by changes in the orientation of chitin microfibrils often form the successive reflecting surfaces giving rise to interference colours. The metallic colours of many beetles, and the iridescence of insect wings are produced in this way. In Lepidoptera, interference colours are produced by the scales, which may have lamellate upper surfaces or rows of cuticular thickenings packed so that they form reflecting surfaces. In this way the blue of *Morpho* is produced. Ultraviolet is produced as an interference colour.

Irregularities at the surface of the cuticle may reflect light, a process known as *scattering*. If the irregularities are large relative to the wavelengths of light, all the light is reflected and the insect appears white; most insect whites are produced in this way. If the irregularities are small, with dimensions approximating the wavelength of blue light (less than 500 nm), only the short wavelengths are reflected. When coupled with a pigment which absorbs the longer wavelengths, as occurs in dragonflies, this process results in a blue colour.

Pigmentary colours. Many types of coloured compounds (pigments) are known. They have in common an extended system of conjugated double bonds. In insects

they are generally present as granules in the epidermis, but melanin is present in the cuticle.

The general brown or black colour of most insect cuticles is at least partly a consequence of sclerotisation. This is why newly moulted insects are usually pale in colour, but become progressively darker in the hours immediately following ecdysis. However, hardening can occur independently of darkening as is evident in albino insects. The quinones used in sclerotisation may polymerise to melanin, a black pigment, in the exocuticle, but although it is very common to infer the presence of melanin (as in melanisation or melanic form) its presence has only been confirmed in a very small number of insects.

The pigments and physical processes which produce the colours of some insects are exemplified in Table 2.1.

RESPIRATORY SYSTEM

In insects, oxygen is conducted directly to the tissues from the environment via a system of tubes, the tracheae; in general, insects do not have a respiratory pigment in the blood.

Tracheal System

The tracheae arise as invaginations of the epidermis, one pair per segment. The invaginations usually join together to form longitudinal trunks from which finer branches extend to the tissues (Fig. 2.10). Terminally, the tracheae are continued as tracheoles, very fine intracellular tubes, less than 1 μm in diameter, which are closely associated with the actively respiring tissues. In flight muscles the tracheoles may indent the muscle plasma membrane (sarcolemma) so that they are functionally intracellular within the muscle fibre, although anatomically the tracheolar and muscle cells remain distinct. This close association reduces the distance over which oxygen must diffuse through the cytoplasm (see below).

The external openings of the tracheae are called spiracles (Fig. 2.11). The greatest number of spiracles present in an insect is 10 pairs, in larvae of bionid flies, but in most insects some reduction in the number occurs. Many aquatic insects have only one pair of functional spiracles, either anterior or posterior in position, with various behavioural or anatomical adaptations which permit gaseous exchange at the water surface while the body of the insect remains submerged. In larval Odonata, Ephemeroptera and Plecoptera the tracheal system is retained although there are no functional spiracles (the apneustic condition). Table 2.2 gives the terminology applied to different numbers and arrangements of spiracles.

In most insects the spiracles have closing mechanisms, often in the form of one or two valves (Fig. 2.12). Closure of the spiracles minimises water loss, and the amount of time for which the spiracles remain open reflects a trade-off between the needs of respiration and the need to reduce water loss. Sequential opening and closing of spiracles also makes it possible for a directed flow of air through the tracheal system to be developed (see below).

The tracheae are lined with cuticle thickened in a spiral band; the thickenings are known as taenidia. They prevent

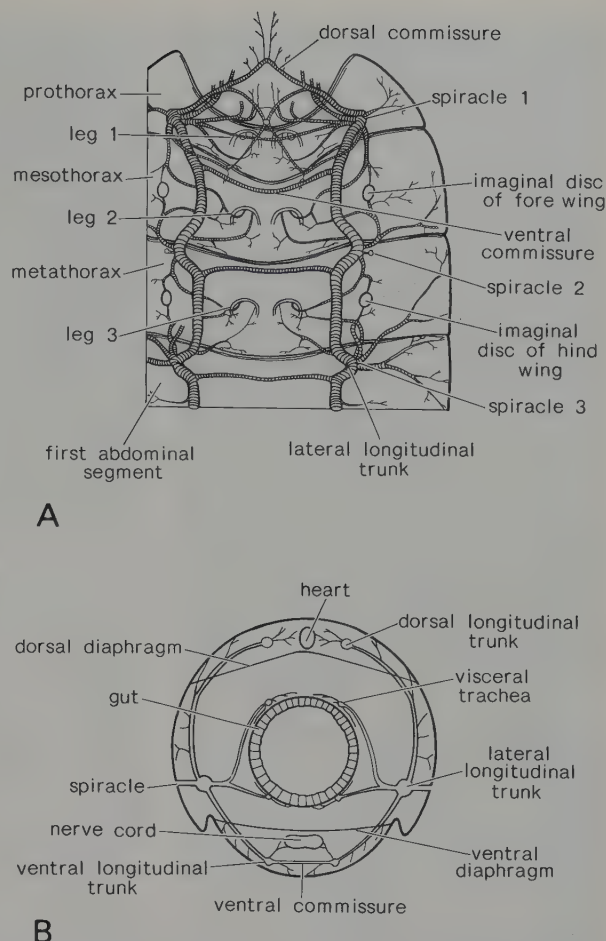


Fig. 2.10 Tracheal system: A, tracheation of thorax and first abdominal segment of caterpillar, dorsal view; B, diagrammatic cross-section of abdomen of orthopteran showing principal tracheae and tracheal trunks. [After Snodgrass in Chapman 1982; A. Hastings]

the tube from collapsing under pressure, while retaining its flexibility. In many insects some tracheae are expanded into bladder-like air-sacs. These too are lined with cuticle, but this lacks the taenidia so the sacs are collapsible. Their principal role is in ventilation (see below).

The cuticular lining of the tracheae is shed and renewed at each moult, the old cuticle being withdrawn through the spiracles. Where the number of spiracles is reduced, moulting is facilitated by withdrawal through otherwise non-functional spiracles. After the moult such non-functional spiracles may be visible as faint scars on the outer segmental cuticle and they remain connected with the tracheae by strands of cuticle. This is true even in apneustic tracheal systems.

Gaseous Exchange

Diffusion. Gaseous exchange normally involves the inward diffusion of oxygen to the tissues and the outward diffusion of carbon dioxide along concentration gradients. The rate of diffusion of oxygen in air is 10 000 times faster than in the tissues. For this reason it is important for the tissue diffusion path to be as short as possible. In flight muscle this is achieved by the tracheoles indenting

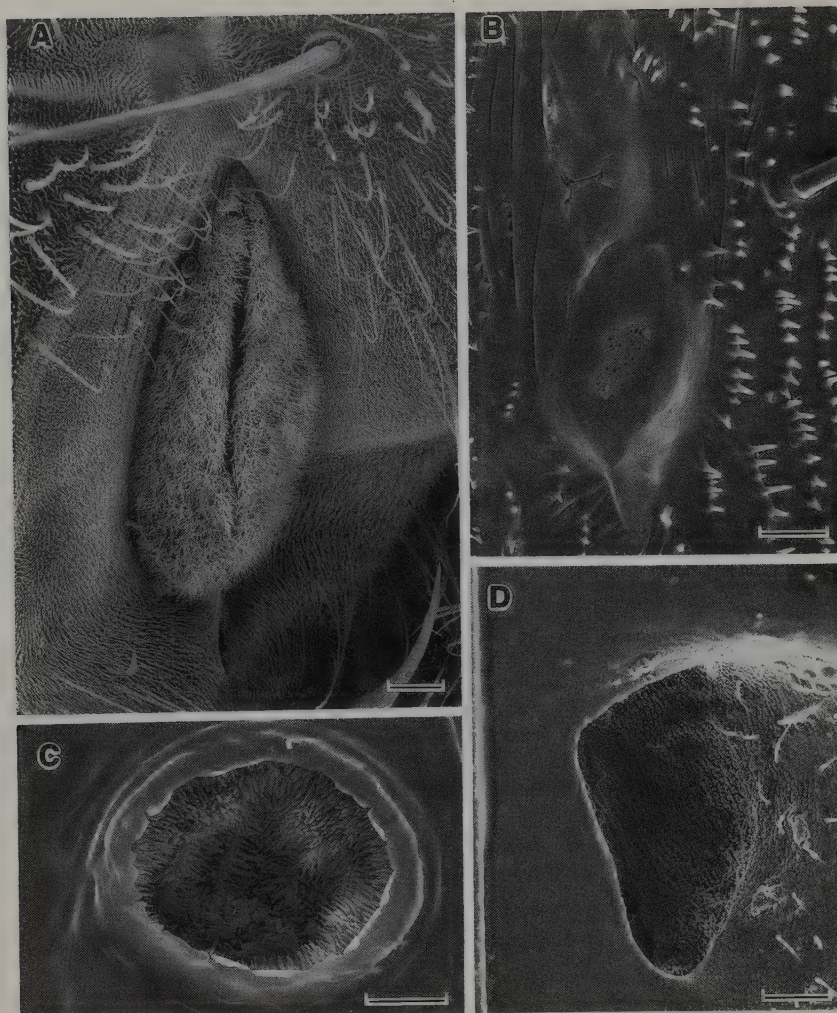


Fig. 2.11 Spiracles: A, *Chrysomya rufifacies* (DIPT: Calliphoridae), adult thoracic spiracle (scale = 50 μm); B, *Lanternarius gemmatus* (COLE: Heteroceridae), larval abdominal spiracle (scale = 10 μm); C, *Corticeus* sp. (COLE: Tenebrionidae), larval thoracic spiracle (scale = 100 μm); D, *Locusta migratoria* [ORTH: Acrididae], abdominal spiracle (scale = 50 μm).

[A, D by C. D. Beaton; B, C by E. Seiling]

Table 2.1 Examples of the physical processes and pigments producing colours in insects

Colour	Pigment and/or Physical Process	Example
BLACK	melanin in cuticle	Diptera, Coleoptera
WHITE	physical scattering: matt white if reflecting surfaces arranged at random; pearly white if they are regular (e.g. overlapping scales on butterfly wing) white pigments also occur: leucopterin supplements physically-produced white	Lepidoptera
RED	carotenoids in many insects ommochromes in many insects ommochromes may also colour internal organs quinones pterins: especially in eye colour	Coccinellidae Odonata, Nymphalidae Coccoidea, Aphidoidea Lepidoptera, Hemiptera
YELLOW	physical interference: brassy yellows carotenoids pterins papiliochromes flavonoids	Lepidoptera Papilionidae Satyrinae
GREEN	physical interference: metallic greens bile pigment bile pigment ?mixed with carotenoids	Lepidoptera, Coleoptera Chironomidae Orthoptera
BLUE	physical interference physical scattering	Lepidoptera Odonata
ULTRA VIOLET	physical interference	Pieridae

Table 2.2 Terminology used in relation to spiracle numbers and arrangement

<i>Polypneustic</i> —at least 8 functional spiracles on each side				
holopneustic	10 spiracles:	2 thoracic	8 abdominal	Acrididae
peripneustic	9 spiracles:	1 thoracic	8 abdominal	cecidiomyiid larvae
hemipneustic	8 spiracles:	1 thoracic	7 abdominal	mycetophilid larvae
<i>Oligopneustic</i> —1 or 2 functional spiracles on each side				
amphipneustic	2 spiracles:	1 thoracic	1 post-abdominal	psychodid larvae
metapneustic	1 spiracle:		post-abdominal	culicid larvae
propneustic	1 spiracle:	mesothoracic		culicid pupae
<i>Apneustic</i> —no functional spiracles				many aquatic larvae

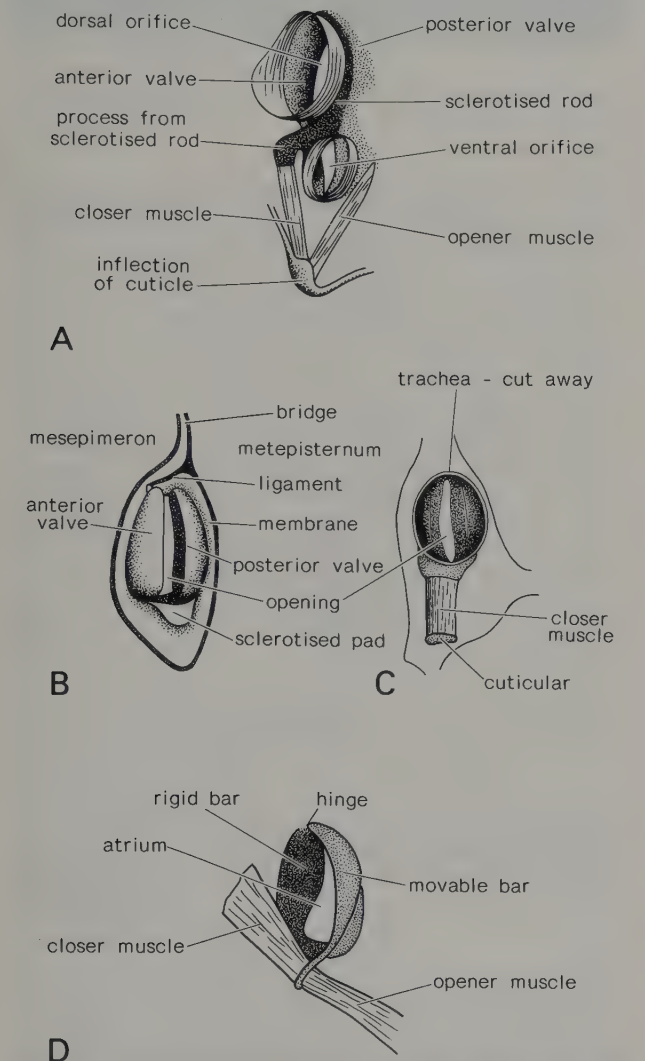


Fig. 2.12 Spiracles: various closing mechanisms in grasshopper spiracles: A, first thoracic spiracle, internal view; B, C, second thoracic spiracle, external and internal views; D, abdominal spiracle, internal. [After Miller, Snodgrass in Chapman 1982; A. Carter, A. Hastings]

the muscle membrane so the diffusion path to the muscle mitochondria is reduced to a few microns.

In aquatic insects with an apneustic tracheal system oxygen diffuses into the tracheae from the surrounding water. This is made possible by the extension of fine, tracheal branches into tracheal gills with a large surface area

and covered by a thin cuticle (Fig. 2.13). Retention of the tracheal system in these insects permits efficient respiration because of the much higher rate of diffusion of oxygen in a mixture of gases (in the tracheae) compared with that in water (in the haemolymph or other tissues). ‘Blood gills’ of mosquito and chironomid larvae are not important in respiration since they do not contain extensive tracheation. Their principal function is in salt regulation.

In some species with tracheal gills movements of the gills maintain a flow of water over richly tracheated areas of the body so that water depleted of oxygen does not accumulate. Rectal ventilation by dragonfly larvae also serves this function; in this case the tracheal gills are in a specialised region of the rectum known as the branchial chamber.

Aquatic insects which dive carrying an air bubble attached to some part of the body, use the bubble as a reservoir of oxygen. It also serves as a temporary gill because oxygen diffuses into the bubble from the water faster than nitrogen diffuses out, so the bubble remains relatively large for a long time. Eventually, however, it becomes so small that the insect is forced to return to the surface.

Other aquatic insects retain a permanent air bubble as a very thin film held in place over the body by hydrofuge, cuticular structures. Such a film is called a plastron and it is only displaced by very high water pressure, through submersion at great depths, or by greatly reduced surface tension, through pollution of the water. Consequently it is, for all practical purposes, permanent and it provides a permanent gill for gaseous exchange with the water; insects with a well-developed plastron, such as the bug *Aphelocheirus* need never come to the surface to renew the bubble. A number of aquatic beetles also have plas-trons. Plastron respiration is also common among insect eggs and the pupae of aquatic insects. The gas film is held by a great diversity of cuticular structures (Fig. 2.14).

Ventilation. In large insects during periods of intense activity, diffusion cannot meet the oxygen requirements of the muscles. Under these circumstances the insect pumps air through the system (ventilation). This is achieved by rhythmically collapsing and expanding the air sacs so that air is alternately forced out of and drawn into the tracheae. The changes in pressure of the air sacs are produced by changes in the body volume, commonly produced by alternately telescoping and extending the abdominal segments, but in flight also resulting from the

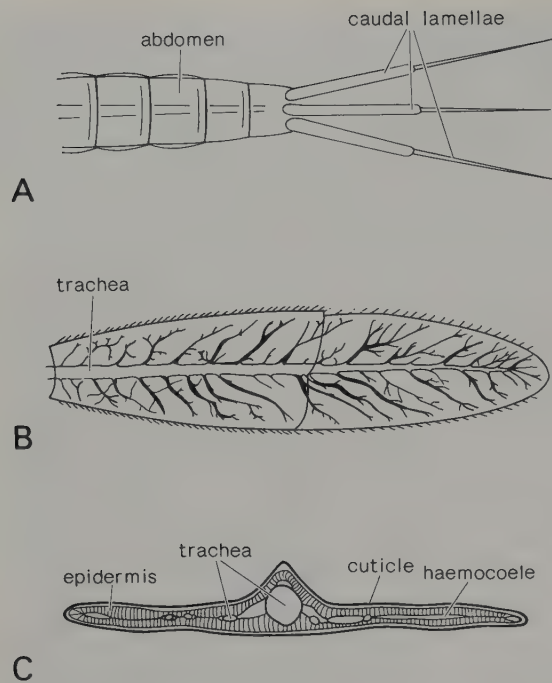


Fig. 2.13 Tracheal gills: A, dorsal view of posterior end of damselfly nymph (after Chapman 1982); B, surface view of one gill (after Gardner in Chapman 1982); C, section through gill (after Tillyard in Chapman 1982).

[L. Warrenner]

rhythmical changes in the volume of the thorax and of the flight muscles themselves. Ventilatory movements are usually associated with rhythmic opening and closing of the spiracles, anterior spiracles opening during inspiration and posterior spiracles during expiration. This produces a flow of air through the tracheal system from front to back and enables the insect to meet the 100-fold increase in oxygen demand by the flight muscles during flight.

NERVOUS SYSTEM

Central Nervous System

The central nervous system comprises a series of ganglia joined together by a pair of longitudinal connectives and giving rise to nerves which extend peripherally to muscles and sense organs. Primitively there is a ganglion in each body segment, but in the postembryonic stages of all insects some degree of fusion of ganglia has occurred. The brain, lying dorsally in the head above the oesophagus, consists of a primitively presegmental cephalic ganglion and at least one postoral segmental ganglion. Three general areas are recognisable within it: the protocerebrum which extends laterally to the optic lobes and the compound eyes; the deutocerebrum, receiving input from the antennae; and the tritocerebrum from which the circumoesophageal connectives extend to the suboesophageal ganglion. The latter is formed by the fusion of the ganglia of the mandibular, maxillary and labial segments and sends nerves to the mouth-parts.

Many insects, such as larval Lepidoptera, have three separate thoracic ganglia, one in each segment, but there are never more than eight abdominal ganglia, the terminal

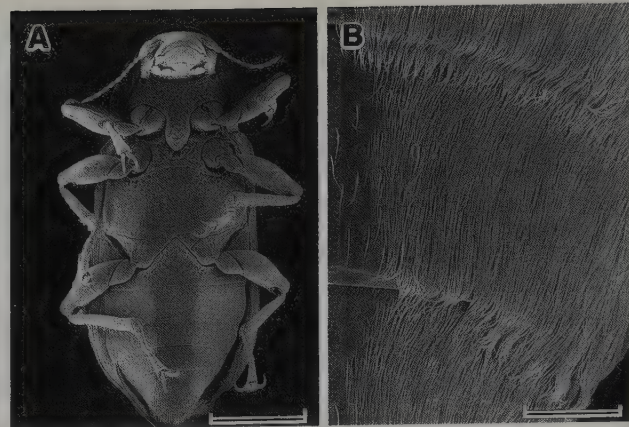


Fig. 2.14 Plastrons: A, *Simsonia tasmanica* (COLE: Elmidae) adult, ventral (scale = 1 mm); B, same, lateral portions of sternites 2-4 (scale = 0.1 mm). [C. D. Beaton]

ganglion always being compound. Varying degrees of fusion of these ganglia occur and in adult Cyclorrhapha, for example, all the thoracic and abdominal ganglia are fused into a single ganglionic mass (Fig. 2.15).

Nerve cells. The basic unit of the nervous system is the nerve cell, or neuron, comprising a cell body with, basically, two projections. One, the dendrite, receives from the environment or other nerve cells a stimulus which causes a change in the electrical potential across the nerve cell membrane. This change in potential leads to the production of short-lived changes in electrical potential, called impulses or spikes, which travel along the second projection, usually very long and known as the axon. Terminally, the axon branches and transmits its information chemically via synapses to the dendrite of another nerve cell (Fig. 2.16) or to an effector organ, usually a muscle.

Nerve cells fall into three classes depending on the source of the input or the destination of the output. Sensory neurons receive stimuli from the environment in the form of light, mechanical distortion or a chemical. They are nearly always situated in the epidermis and associated with some modification of the cuticle permitting the stimulus to interact with the nerve cell. Their axons then pass without interruption to the central nervous system where they synapse, usually, with interneurons.

Interneurons are nerve cells which are stimulated chemically by nerve cells and transmit information, also chemically, to other nerve cells. Motor neurons receive information from interneurons and transmit it to muscles, so it is the activity of these cells which ultimately leads to muscular contraction. Chemical transmission between nerve cells is believed to involve acetylcholine, while neuromuscular transmission uses glutamate. Other transmitter substances are also known.

The cell bodies of interneurons and motoneurons are aggregated together with the extensive synaptic interconnections of all types of nerve cells to form the ganglia.

Blood-brain barrier. The central nervous system is surrounded by a sheath of connective tissue and peri-

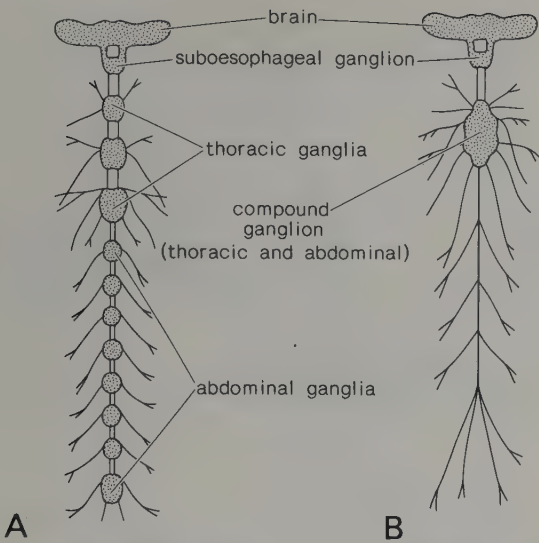


Fig. 2.15 Central nervous system: two extreme arrangements of ganglia showing minimal (A) and maximal (B) degrees of fusion.
[After Horridge in Chapman 1982; A. Carter]

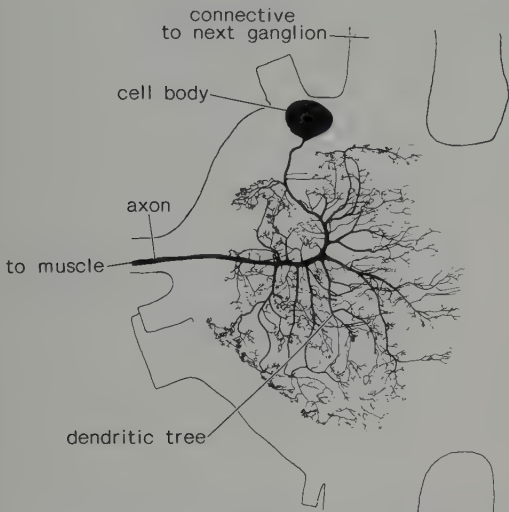


Fig. 2.16 Central nervous system: diagram of mesothoracic ganglion of *Chortioctetes* (ORTH), showing extensive dendritic branching of motoneuron controlling dorsoventral flight muscle (after Altman and Tyrer in Barton Browne 1974).

neurial glial cells. These cells form a barrier between the nerve cells and the haemocoel—the ‘blood–brain barrier’—which is critically important for the functioning of the nervous system. Conduction along an axon involves potassium and sodium ions, while amino acids act as neurotransmitters at some synapses. These substances are present in the haemolymph which varies in composition. The blood–brain barrier ensures that the nerve cells function in a constant environment, unaffected by variations in the haemolymph.

Function. The central nervous system controls the activities of all skeletal musculature. In a few cases simple reflex arcs, direct connections between sensory and motor cells, are known to exist, but most insect behaviour is a consequence of complex integration of information

within the central nervous system. The brain is the major integrative center and, in the intact insect, probably all activities are commanded and modulated by the brain.

The precise patterning of muscle contractions in a particular movement may, however, be regulated within postcephalic ganglia. For example, the activity of the flight muscles in flight is regulated from within the thoracic ganglia; the rhythmic muscular activity associated with oviposition by grasshoppers is controlled by neurons in the terminal abdominal ganglion.

Stomodaeal Nervous System

A series of small ganglia on the surface of the fore gut (Fig. 2.17) are involved in regulating the activity of the fore gut musculature. The ganglia, with their connecting nerves, form the stomodaeal (also known as stomatogastric) nervous system. They are closely associated with the corpora cardiaca and corpora allata, parts of the endocrine system, and sometimes these two glands with the hypocerebral ganglion are referred to as the retrocerebral system.

SENSE ORGANS

Mechanoreception

Touch. Physical contact with environmental features (the sense of touch) is monitored by hair (trichoid) sensilla (Fig. 2.18). These are scattered over the surface of the body and many of the hairs used by taxonomists are mechanoreceptors. These hairs are innervated by a single neuron and bending the hair from the base deforms the sensory dendrite producing a depolarisation of the cell and a train of spikes to the central nervous system. In most instances stimulation only occurs during bending; sensory input ceases during static deflection.

Hearing. Aerial vibrations are perceived by various sensilla. In crickets and caterpillars, long slender trichoid sensilla respond to the movement of the air. In other cases the movement of the air causes a membrane, the tympa-

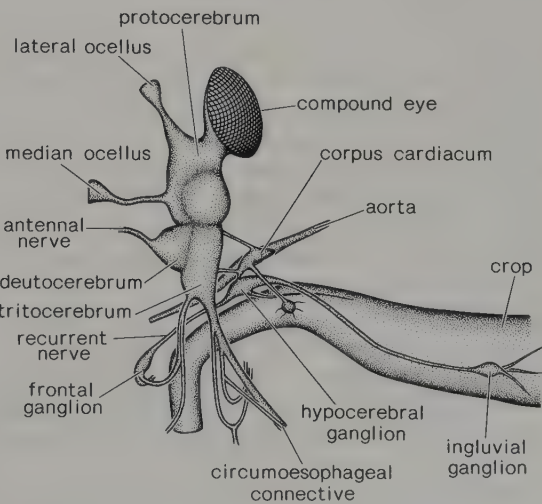


Fig. 2.17 Nervous system: brain and stomodaeal nervous system of *Locusta*.
[After Albrecht in Chapman 1982; A. Carter]

num (Fig. 2.19), to vibrate and these vibrations are perceived by chordotonal organs which are subcuticular. In most cases the tympanum is backed by a large air-sac so that it vibrates more freely than would be the case if it was in direct contact with the haemolymph. In tettigoniids and crickets sound waves are also carried via a large trachea to the inside of the tympanum. Each chordotonal organ is made up of one or more units, called scolopidia (Fig. 2.20A), which consist of three cells arranged in a linear manner. The dendrite of the nerve cell ends in a sheath, or scolopale, cell and this is attached to the underside of the tympanum by an attachment, or cap, cell.

Tympanal organs occur on the prothoracic legs of Grylloidea and Tettigonioidae, on the mesothorax in some Hydrocorisae, on the metathorax in Noctuidae and on the abdomen in Acrididae, Cicadidae, Pyraloidea and Geometroidea. In *Chrysopa* the tympanum is on the fore wing. The number of scolopidia associated with the tympanum varies from one in *Plea* to about 1500 in Cicadidae.

The tympanal organs of different groups of insects respond to a wide range of frequencies. Gryllids and cicadas respond to sounds with frequencies from 100 or 200 Hz to 15 kHz, similar to the range of human hearing. Grasshoppers extend up to about 50 kHz and tettigoniids to about 100 kHz, well into the human ultrasonic range. These different ranges of sensitivity reflect the ranges of sounds produced by conspecifics since the primary function of the auditory system of these insects is in reproductive behaviour. The auditory systems of moths and lacewings, by contrast, are adapted to the avoidance of insectivorous bats, hunting by means of ultrasound. Noctuids are sensitive to sounds with frequencies up to 240 kHz.

Although some degree of frequency discrimination is possible, most insects are sensitive to and respond to the temporal patterning of conspecific song rather than the frequency components.

A chordotonal organ is also inserted into the base of the antennal flagellum (Fig. 2.20B). It is known as Johnston's organ and is present in all adult insects and many larvae but is absent from Collembola and Diplura. It perceives movements of the flagellum relative to the pedicel. In male Culicidae and Chironomidae it perceives the sounds produced by the wings of females in flight; in other insects it is known to have a role in monitoring and regulating the speed of the insect through the air.

Vibrations carried through the substratum are also perceived by chordotonal organs. These occur in the proximal part of the tibia and are known as subgenual organs. They are not associated with a joint and usually contain between 10 and 40 scolopidia. Subgenual organs are very sensitive and in *Periplaneta* respond to displacements of 10^{-7} cm or even less over a range of frequencies up to 8 kHz. Coleoptera and Diptera have no subgenual organs; substrate vibrations are perceived by other, less sensitive sensilla.

Proprioception. Various types of mechanoreceptors function as proprioceptors.

Groups of small trichoid sensilla, present at joints in

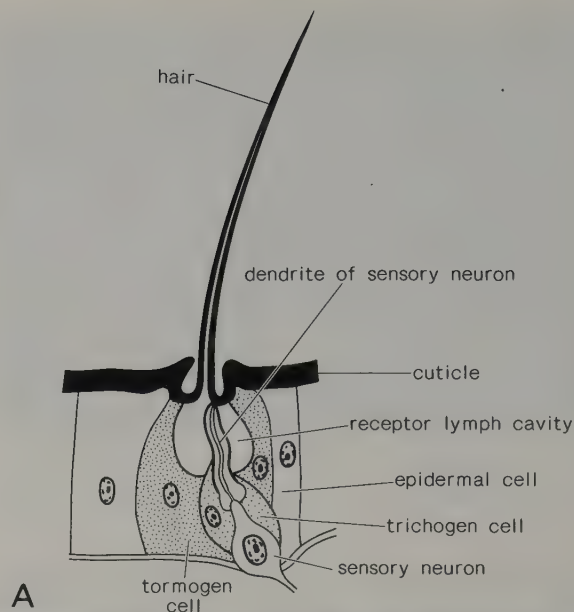


Fig. 2.18 Mechanoreception: A, diagram showing arrangement of cells associated with trichoid mechanoreceptor; B, trichoid sensilla on abdomen of *Chrysomya rufifacies* (DIPT: Calliphoridae) (scale = 50 μ m). [A by A. Carter; B by C. D. Beaton]

the skeleton, are stimulated when one part of the cuticle is flexed against another (Fig. 2.21). Unlike trichoid sensilla with an exteroceptive function, their neurons continue to fire during static deflection. They thus monitor the position of one part of the body relative to another. They are

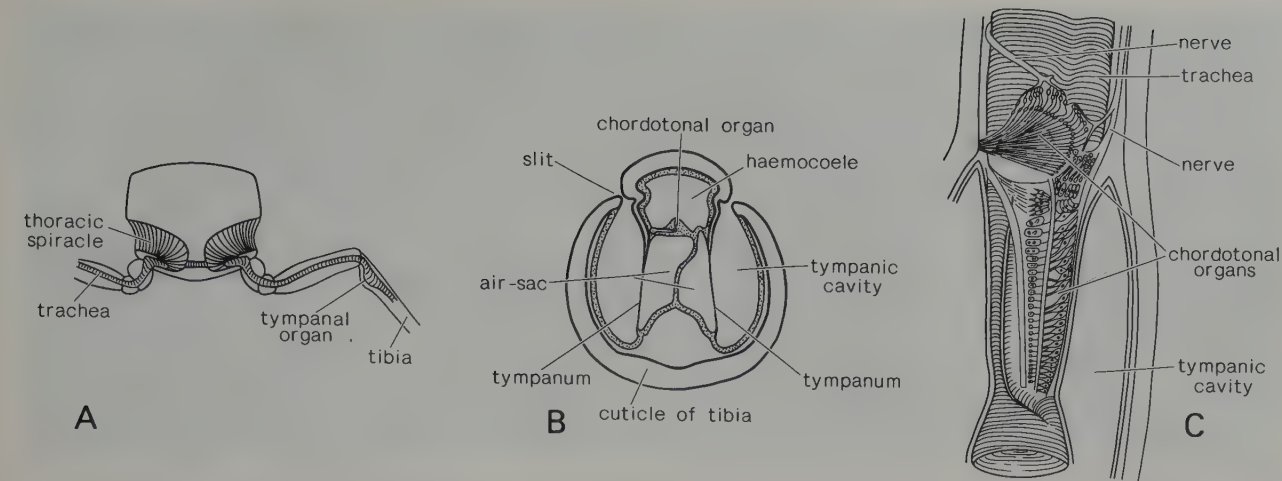


Fig. 2.19 Mechanoreception: tympanal organ of tettigoniid: A, section through fore legs and thorax, showing wide trachea acting as 'hearing trumpet'; B, transverse section of anterior tibia showing two tympani; C, longitudinal section of tibia, showing chordotonal organs associated with tympani. [After Michelsen and Larsen 1985; A. Carter]

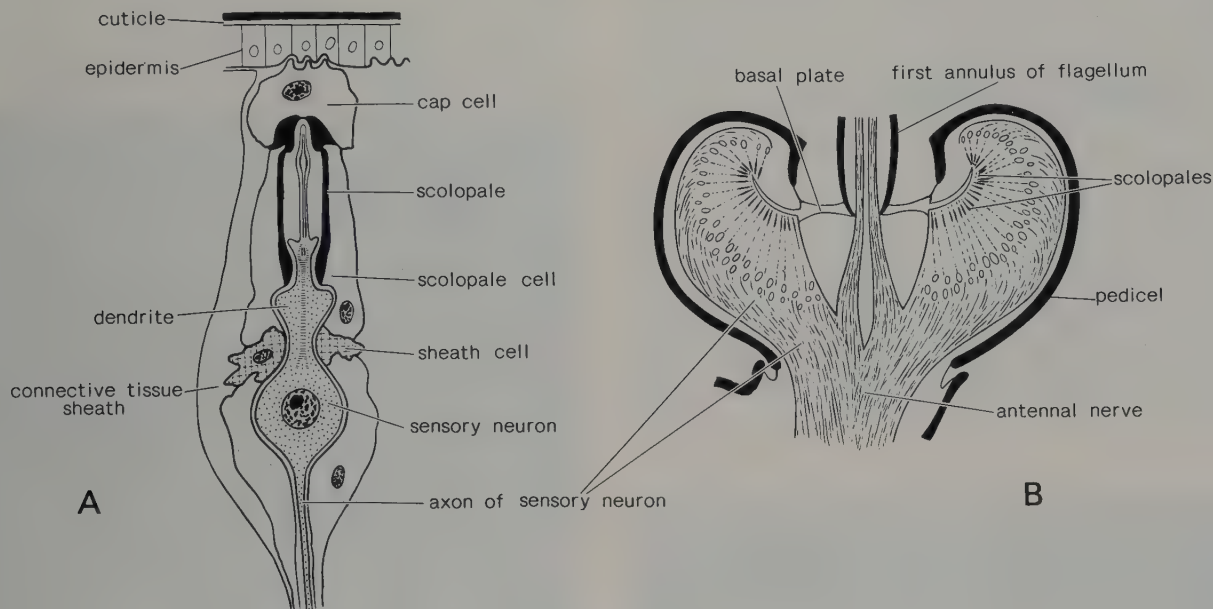


Fig. 2.20 Mechanoreception: A, scolopidium (after Gray 1960); B, Johnston's organ (after Child 1894). [A. Carter]

found at leg joints, at the bases of the antennae, on the cervical sclerites and elsewhere.

Stress due to distortion of the cuticle is monitored by campaniform sensilla. These comprise domes of very thin cuticle, usually oval in outline, with a single neuron inserted into the centre of the dome (Fig. 2.22). Distortion of the cuticle causes the dome to bow upwards and this is the effective stimulus. Campaniform sensilla of different sizes, and presumably with different sensitivities, occur in groups near leg joints, on the mouth-parts, and at the bases of the wings.

A fundamentally different type of proprioceptor is the stretch receptor. This is an internal structure associated with muscles or connective tissue. Stretch receptor neurons are multipolar with numerous dendritic endings inserted into a fibre tract. Changes in the length of the

fibre tract produce changes in the rate of firing of the nerve cell. Stretch receptors commonly occur in the inter-segmental muscles of the abdomen and in the wall of the gut. They provide information on the position, or degree of distension, of a part of the body and can also monitor slow, rhythmic movements such as ventilatory movements.

Chemoreception

Taste. Contact chemoreceptors are most abundant on the mouth-parts, but they are also present on the antennae and tarsi and often are found elsewhere on the body. Insect contact chemoreceptors respond to contact with dry chemicals, such as those on a leaf surface, as well as chemicals in solution. They are sensilla with a terminal pore through which the stimulating chemical passes to

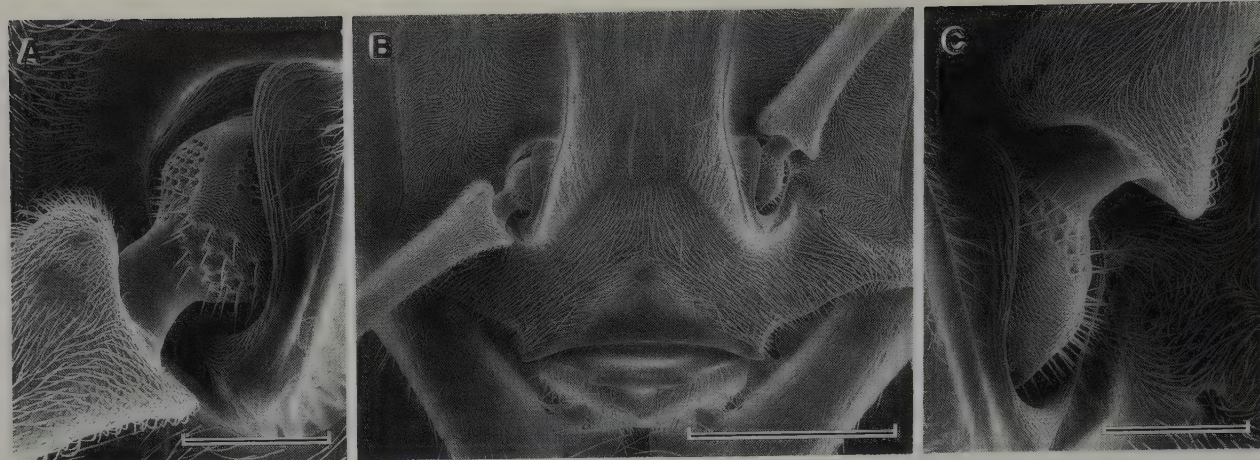


Fig. 2.21 Proprioception: A–C, hair plates at bases of antennae in *Myrmecia pyriformis* (HYMN: Formicidae) (scales for A and C = 0.2 mm; for B = 1 mm). [C. D. Beaton]

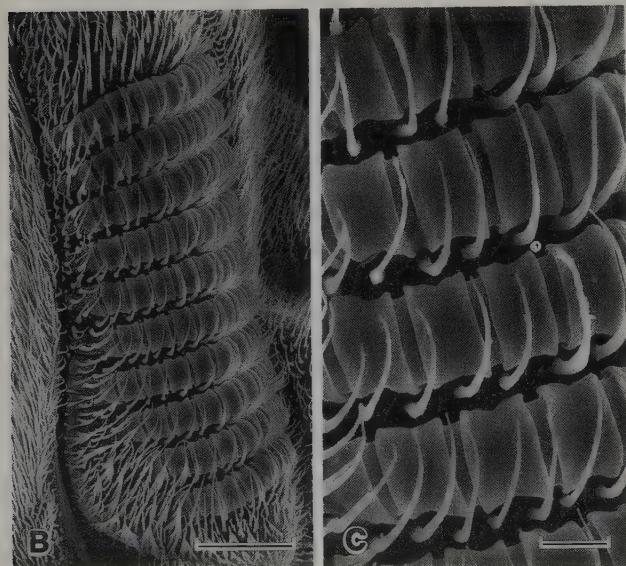
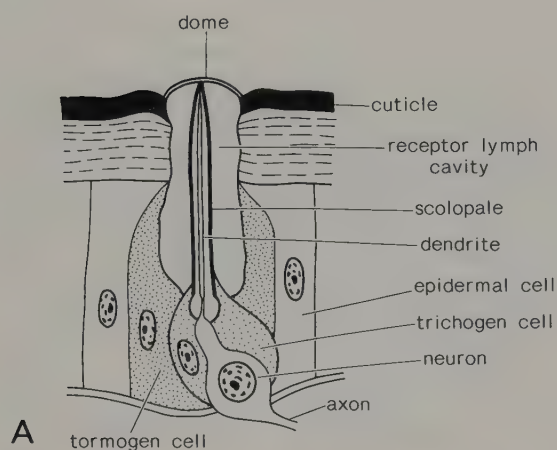


Fig. 2.22 Proprioception: A, diagram showing arrangement of cells forming campaniform sensillum; B, C, field of campaniform sensilla at base of haltere in *Sarcophagid* sp. (DIPT: Sarcophagidae) (scale for B = 20 μ m, for C = 5 μ m). [A by A. Carter; B, C by C. D. Beaton]

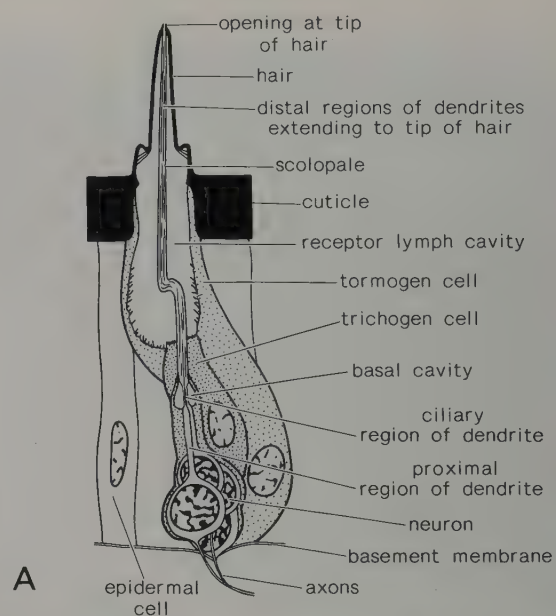


Fig. 2.23 Taste: A, diagram showing arrangement of cells forming contact chemoreceptor (after Slifer *et al.* in Chapman 1982); B, contact chemoreceptor on antenna of *Vespula germanica* (HYMN: Vespidae) (scale = 2 μ m). [A by A. Carter; B by C. D. Beaton]

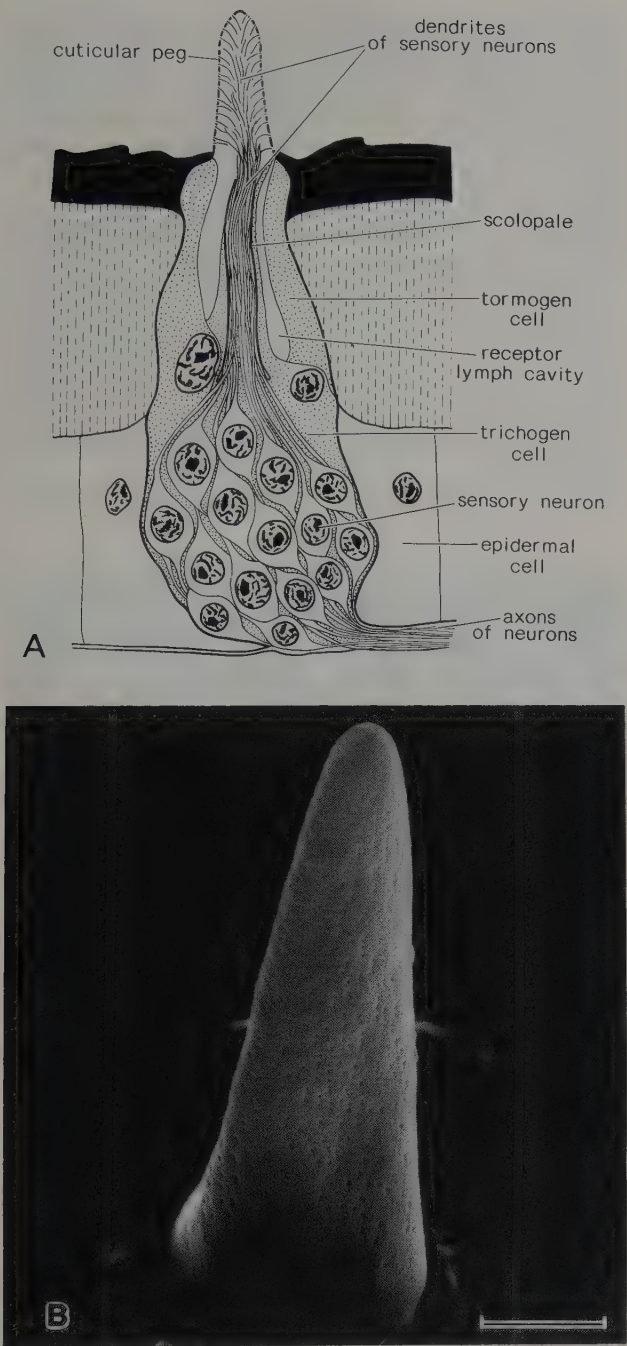


Fig. 2.24 Smell: A, diagram showing arrangement of cells forming olfactory sensillum (after Slifer et al. 1959); B, olfactory sensillum on antenna of *Locusta migratoria* (scale = 2 μ m). [A by A. Hastings; B by C. D. Beaton]

reach the sensory dendrites which end just inside it (Fig. 2.23). The sensilla are usually hairs or cones and commonly possess four, sometimes more, neurons. It is often true that these neurons have different ranges of sensitivity so that in caterpillars it is often possible to recognise separate cells responding electrophysiologically to sugars, salts, water and, perhaps, deterrent compounds. In other groups of insects the functional distinctions between neurons may be less well marked.

Smell. Insect olfactory sensilla are characterised by the presence of numerous, small pores in the cuticle through which odour molecules diffuse to the dendrite endings (Fig. 2.24). The cuticular structure is often in the form of a short peg (basiconic), but may be a flat plate (plate organ) or may be sunk into a pit (coeloconic). There may be from one to over 40 neurons in each sensillum. Most olfactory sensilla are present on the antennae and their number may be very large (Fig. 2.25). On the antenna of the cockroach, *Periplaneta*, there are about 100 000 olfactory sensilla; in the male of the moth, *Bombyx*, there are about 25 000. The very large number of sensilla enables the insect to detect odours in very low concentrations by increasing the chances of contact with an odour molecule.

The neurons in some olfactory sensilla may be highly sensitive to specific odours. This is mainly true of neurons which are sensitive to sex pheromones. For example, the pheromone-sensitive neurons in the male *Trichoplusia ni* are 300–2000 times more sensitive to the female pheromone *cis*-7-dodecanyl acetate than to its *trans* isomer. Other cells have broad spectra of sensitivity enabling the insect to be aware of, and have the potential to respond to, other odours in the environment.

Thermoreception

Insect behaviour is greatly affected by the temperature. This is partly a consequence of the link between body temperature and metabolic activity, but neural activity is also temperature sensitive. In addition, many insects are known to have temperature receptors. These are often housed in small peg-like sensilla without pores on the antennae. They are often most sensitive to falling temperature.

Vision

Compound eyes. The principal organs of vision of adult insects and larval exopterygotes are the compound eyes (Fig. 2.26). These are made up of a number of similar units, the ommatidia (Fig. 2.27). Each ommatidium comprises a lens system and, typically, eight light-sensitive retinula cells grouped round the long axis of the unit. The cell membrane of each retinula cell on the side nearest the ommatidial axis is produced into an array of close-packed microvilli orientated at right angles to the long axis of the cell. The microvilli of a cell are said to form the rhabdomere, while the rhabdomeres of all the retinula cells collectively form the rhabdom (this terminology derives from the time when the rhabdom was believed to be an independent structure). In dayflying insects the rhabdom extends to the crystalline cone of the lens system; eyes with this arrangement are called apposition eyes. In crepuscular and nocturnal insects, the rhabdoms are short and separated from the crystalline cones by a clear zone, hence clear-zone eyes. Between adjacent ommatidia are pigment cells, while externally the ommatidia are distinguished by the hexagonal facets formed by the cuticular (corneal) lenses (Fig. 2.26). Most compound eyes contain some hundreds of ommatidia, but the num-

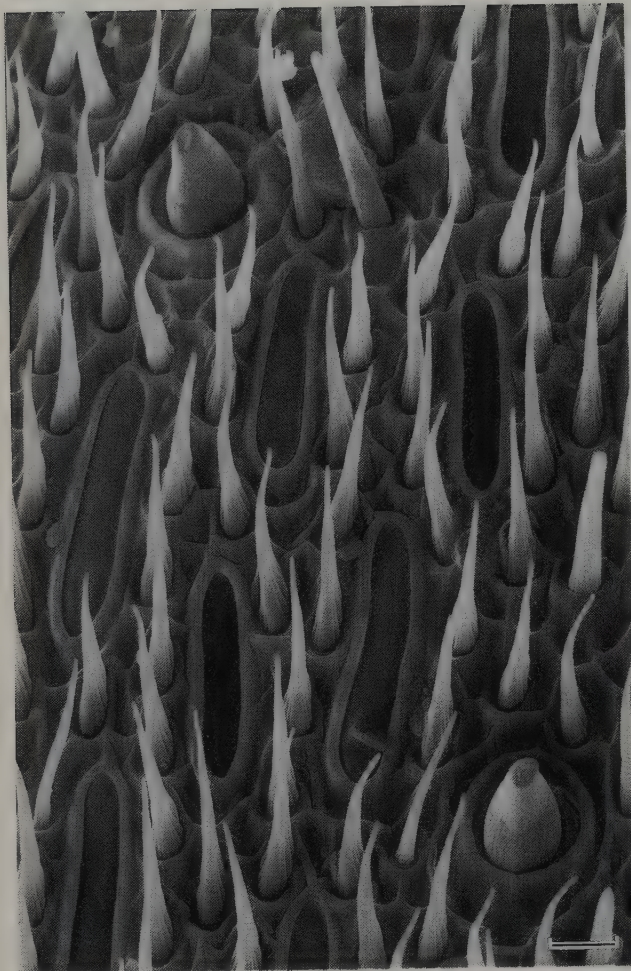


Fig. 2.25 Smell: one annulus from antenna of *Vespula germanica* (HYMN: Vespidae), showing large number of olfactory sensilla (scale = 5 μ m). [C. D. Beaton]

ber ranges from one in *Hypoconera punctatissima* to over 10 000 in the eyes of dragonflies.

In apposition eyes each ommatidium is so completely surrounded by pigment that the rhabdom only receives light from its own lens system which only transmits light effectively if the light rays are within about 1° of its long axis. Hence each rhabdom will receive light from only a limited part of the visual field with relatively little overlap with adjacent rhabdoms and the eye as a whole will receive a sharp image made up of a mosaic of spots of differing intensity, each spot being formed in an individual ommatidium.

An image may be formed in the same way in light-adapted clear-zone eyes in which screening pigment extends between the ommatidia. In the formation of such an image, however, much light which enters the eye is lost, being absorbed by the screening pigment. Under conditions of low light intensity the eye becomes dark adapted by withdrawal of the screening pigment. This permits light to pass obliquely through the clear zone so that light from a single lens system may reach the rhabdoms of several different ommatidia. This increases the sensitivity of the eye at the expense of visual acuity.

The visual pigment is present in the membrane of the microtubules of the rhabdomeres. It is derived from vitamin A. When light of an appropriate wavelength is absorbed by a molecule of visual pigment, the molecular configuration of the molecule changes, releasing energy which causes a depolarisation of the retinula cell membrane.

Colour vision has been demonstrated in insects belonging to all the major orders. This ability depends on the possession of visual pigments with maximum sensitivity to light of different wavelengths; very often there are three different pigments. Only one type of visual pigment occurs in any one retinula cell. In general, insects exhibit greater sensitivity at the blue end of the spectrum than at the red end, and in some cases this sensitivity extends to the ultraviolet.

Ocelli. In addition to the compound eyes, many insects

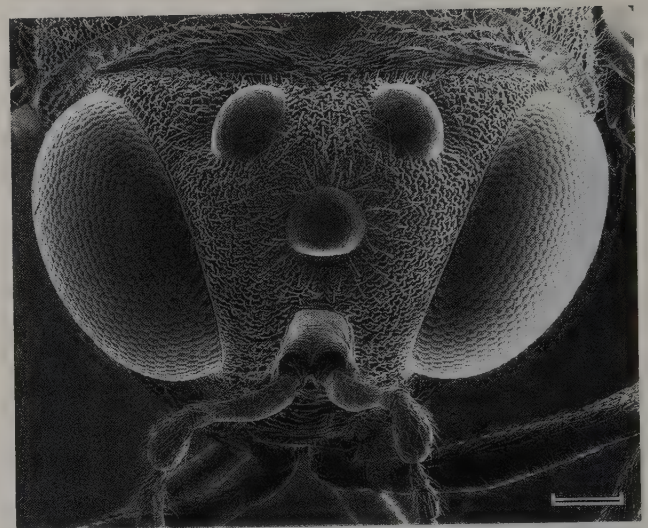


Fig. 2.26 Vision: *Smicromorpha* sp. (HYMN: Chalcididae), anterdorsal view of head, showing compound eyes and ocelli (scale = 0.1 mm). [E. Brooks]

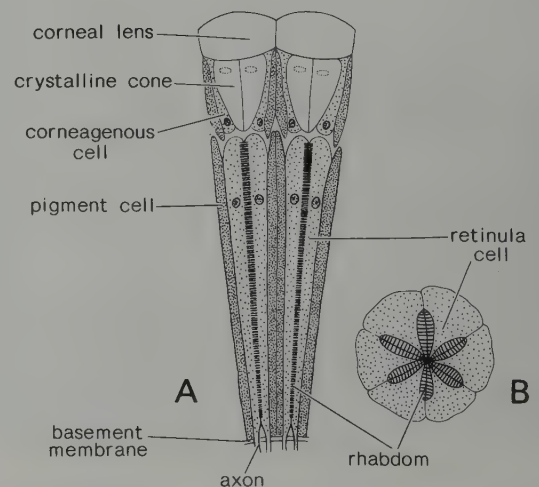


Fig. 2.27 Vision: compound eye: A, diagrammatic, longitudinal section showing structure of two ommatidia; B, diagrammatic, transverse section of ommatidium.

have three ‘simple’ eyes, or ocelli, forming an inverted triangle anterodorsally on the head (Fig. 2.26). They are not present in the larvae of holometabolous insects or in wingless adults, and even in winged insects may be reduced in number, or absent.

Each ocellus comprises an area of transparent cuticle, which is sometimes lens-shaped, backed by several hundred retinula cells. Groups of adjacent retinula cells form rhabdoms, as in the compound eyes (Fig. 2.28B).

The precise functions of the ocelli still remain unclear.

Stemmata. These are the visual organs of the larvae of holometabolous insects. They occur laterally on the head and vary in number from one on each side in tenthredinid larvae to six on each side in caterpillars. In some insects the structure is similar to that of adult ocelli (Fig. 2.28A), but in others there is a single rhabdom and a crystalline lens beneath the cuticular lens. Stemmata, singly or collectively, are capable of some limited form perception.

SOUND PRODUCTION

Many insects produce sounds, sometimes simply as a by-product of some other activity such as flight, but often by some special mechanism. These mechanisms include: banging part of the body against the substratum, as in the death watch beetle; forcing air out of the alimentary canal, or the tracheal system, as in the cockroach *Gromphadorhina*; rubbing one part of the body against another (frictional methods); or vibrating a membrane by direct muscular activity. The two last are the best known.

In insects producing sound by friction it is usually possible to distinguish a file (strigil), usually a series of ridges, from a scraper (plectrum). Movement of the scraper over the file causes the membrane to which the file is attached to vibrate and so to produce a sound. Frictional sounds are produced by species in many orders and many different parts of the body are modified to form the file and scraper, but they are particularly common in Orthoptera, Heteroptera and Coleoptera. In Grylloidea and Tettigonioidea one or both tegmina possess a file at the base of the cubital vein which rasps against a scraper on the other wing (Fig. 2.29A). In crickets the sound frequency depends on the frequency with which file teeth strike the scraper, whereas in tettigoniids each tooth impact causes the tegmen to vibrate with its own natural frequency. Very high frequency sounds, up to 100 kHz, are produced as a result. In brachypterous species sound production is the primary, if not the only function of the tegmina. Many Acridoidea produce sounds with a femoral file; in this case a series of short pegs rasps against the tegmen. In most other groups the stridulatory

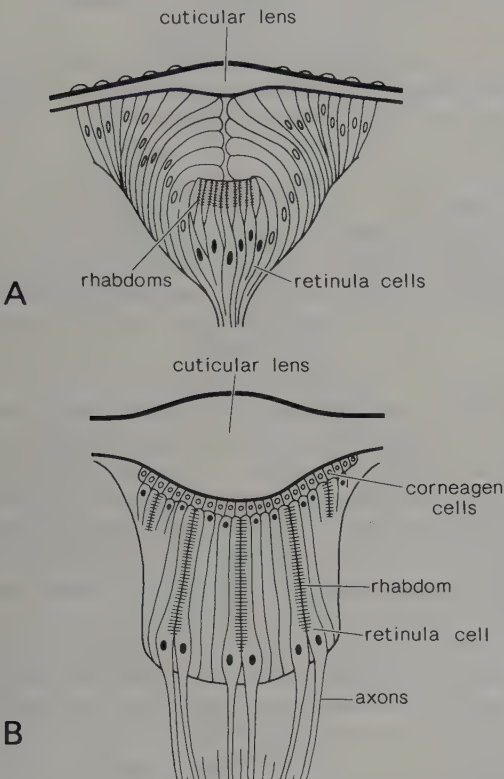


Fig. 2.28 Vision: A, diagram of larval *Dytiscus* (COLE: Dytiscidae) (after Grenacher 1879); B, diagram of ocellus of adult dragonfly (ODON: Libellulidae) (after Ruck and Edwards 1964).

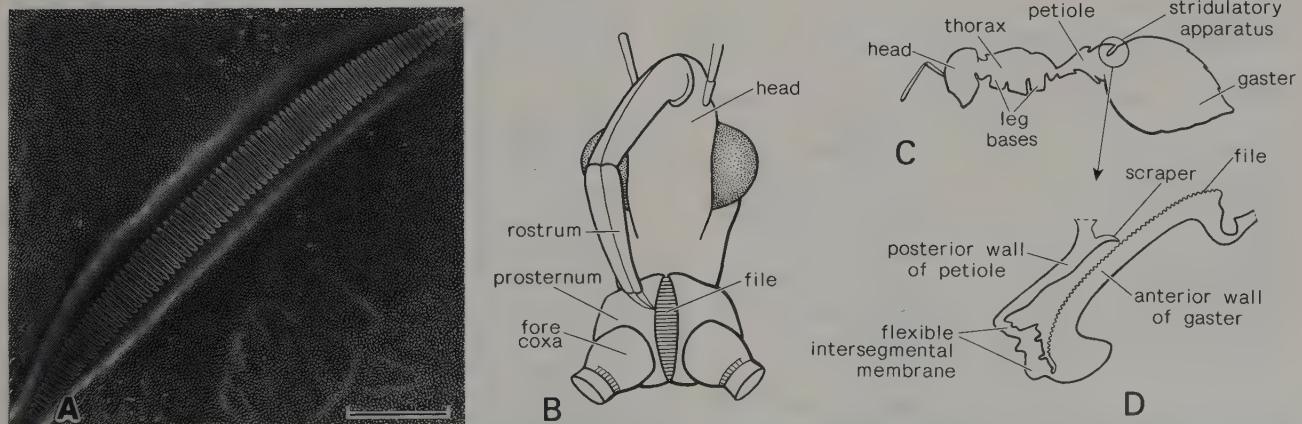


Fig. 2.29 Sound production: A, stridulatory file under left tegmen in a species of Tettigoniidae (ORTH) (scale = 0.5 mm); B, ventral view of head and prosternum in *Coranus* sp. (HEMI: Reduviidae), showing tip of rostrum rasping against intercoxal file; C, D diagram showing position and form of stridulatory apparatus in *Myrmecia* (HYMN: Formicidae). [A by C. D. Beaton; B–D by A. Hastings after Dumortier in Chapman 1982]

mechanism does not involve the wings (Figs 2.29B, c) and the sound produced is of relatively low intensity because of the absence of a large, freely vibrating membrane.

Various Auchenorrhyncha produce sounds with a vibrating membrane, and a similar mechanism is employed by a few Heteroptera and Lepidoptera. In cicadas a large area of thin cuticle, the tymbal, on the first abdominal segment is held taught by a rigid, cuticular frame. It is backed by an air-sac and has a large muscle inserted by a slender apodeme near its centre (Fig. 2.30). When the muscle contracts it pulls the tymbal inwards, distorting it slightly; on relaxation of the muscle the tymbal clicks out again. Each inward or outward movement of the tymbal produces a pulse of sound at a frequency determined by the natural frequency of the tymbal. The muscle contracts at high frequencies so that sound pulses may be produced at frequencies as high as 400 Hz. In some cicadas the tymbal muscles are fibrillar muscles, but this is not true of all species.

Sounds are used in reproductive behaviour and, in social insects, for communication associated with other activities; they are also used in defence.

ENDOCRINE SYSTEM

While the minute by minute behaviour of insects is controlled by the central nervous system, long term changes in form and function are regulated by hormones. The occurrence of some behaviour patterns, such as ecdysis, are also hormonally regulated. A few of the activities regulated by hormones are shown in Table 2.3.

Some hormones are produced in discrete endocrine glands. Moulting hormone is produced by diffuse structures at the back of the head or in the thorax known as the prothoracic, or thoracic, glands. They show cycles of development associated with hormone production and usually disappear after the final moult. The corpora allata are a pair of small discrete glandular organs, one on either side of the fore gut; they produce juvenile hormone. The corpora cardiaca are glands on either side of the aorta just behind the brain; they produce, for example, adipokinetic hormone.

Most hormones, however, are produced by cells within the ganglia of the central nervous system. These are

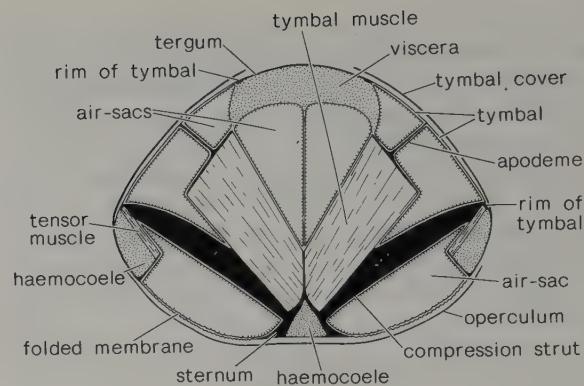


Fig. 2.30 Sound production: diagrammatic transverse section of first abdominal segment of cicada, showing main structures concerned with sound production (after Pringle in Chapman 1982). [A. Carter]

called neurosecretory cells and they can be visualised in histological sections by specific stains. The secretions, and associated carrier proteins, are produced in the cell bodies and then carried along the axons to specific release sites where the hormone is liberated into the blood. The corpora cardiaca, as well as being true endocrine glands, are release sites (neurohaemal organs) for hormones produced by the neurosecretory cells of the brain. The hormones accumulate and are stored in the corpora cardiaca until their release into the blood is triggered via the nervous system. Other neurohaemal organs occur on the peripheral nerves in the abdomen, releasing hormones produced in the segmental ganglia. In some cases neurosecretions pass directly to their target organs along the axons, without ever entering the blood.

Hormones are varied in their chemical structures. Ecdysones are steroids and, since insects are unable to synthesise steroids *de novo*, their production depends on a dietary source of steroid. Juvenile hormone is a terpenoid, while the various neurosecretions which have so far been characterised are peptides or small proteins.

MUSCLES

Structure

Insect skeletal muscles do not differ in their basic structure from the striated, skeletal muscles of other animals.

Table 2.3 Examples of some activities affected by hormones

Activity	Hormone	Chemical nature	Origin
Moulting (initiation)	prothoracicotropic hormone	protein	neurosecretory cells in brain
Moulting	ecdysone	steroid	prothoracic gland
Larval tissue production	juvenile hormone	terpenoid	corpora allata
Ecdysis	eclosion hormone	peptide	neurosecretory cells in brain
Sclerotisation	bursicon	peptide	neurosecretory cells in brain or ventral ganglia
Oogenesis	juvenile hormone	terpenoid	corpora allata
Lipid mobilisation	adipokinetic hormone	peptide	corpora cardiaca
Diuresis	diuretic hormone	peptide	neurosecretory cells in brain or ventral ganglia

The contractile units comprise myosin filaments each surrounded by a ring of six actin filaments. These are aligned across the muscle fibre in sarcomeres, separated by Z-discs, giving the muscle a striated appearance histologically. In most muscles the fibrils are small, the isotropic (I) bands constitute up to 30% of the sarcomere length, and sarcoplasmic reticulum is extensive. But in insects with a high wingbeat frequency the flight muscles are usually specialised, fibrillar muscles. In these the fibrils are up to 5 µm in diameter and the fibres are correspondingly large, sometimes exceeding 1 mm in diameter, the I band constitutes less than 10% of the sarcomere length, and the sarcoplasmic reticulum is greatly reduced.

The visceral muscles associated with the alimentary canal, the heart and some other tissues are also striated, unlike the smooth visceral muscles of vertebrates, but they commonly have 12 actin filaments round each myosin filament and the fibres may branch and anastomose. Some muscles have the capacity for supercontraction, shortening to less than the length of the A-band which is the limit in most skeletal muscle. These muscles allow for a big variation in the size of an organ such as the crop.

Function

A muscle is stimulated to contract by the arrival of a nerve impulse at the nerve-muscle junction. Insect muscles differ from those of vertebrates in that the change in the electrical potential which this produces in the muscle membrane rapidly decays; it does not spread over the whole membrane. Consequently, insect muscles are characterised by the presence of numerous nerve endings derived from the branching of a single axon. This is called multiterminal innervation.

The number of independent functional units in an insect muscle is small compared with vertebrates and this potentially limits the gradations of force which a muscle can exert. However, gradation is achieved by innervation of each muscle unit by up to three different motor neurons with different properties. Some leg muscles, for example, are innervated by a fast axon, a slow axon and an inhibitory axon, such innervation being called polyneuronal. 'Fast' and 'slow' do not refer to the speeds of conduction along the axon, but to the nature of the electrical changes produced in the muscle membrane and the associated contraction. Stimulation via the fast axon produces a powerful, ungraded contraction of the muscle, whereas stimulation via the slow axon produces a contraction whose strength is proportional to the rate of stimulation. Finally, stimulation via the inhibitory axon causes the muscle to relax. This arrangement provides the insect with considerable versatility of muscular output despite the limitation of the number of units.

In most muscles, including the flight muscles of Odonata, Blattodea, Mantodea, Orthoptera and Lepidoptera, there is a direct 1:1 relationship between stimulation via an excitatory axon and muscle contraction; these are called synchronous muscles. However, in fibrillar muscles the frequency of muscle contraction exceeds the frequency of nervous stimulation. Nerve impulses initiate

and subsequently maintain muscle contraction, but the frequency of contraction is governed by the physical properties of the cuticular system which is moved. Such muscles are said to be asynchronous and they usually oscillate at high frequencies. The flight muscles of Hemiptera, Diptera, Hymenoptera and Coleoptera are fibrillar and asynchronous; so are the tymbal muscles of some cicadas.

Arrangement

Muscles are arranged segmentally with dorsal and ventral longitudinal muscles running from one segment to the next and dorsoventral muscles passing from tergum to pleuron or sternum within a segment (Fig. 2.31). This basic plan is repeated in each segment of the thorax and abdomen. Other arrangements occur in the head, associated with the mouth-parts, in the thorax associated with the legs, and in the terminal abdominal segments, in association with the genitalia.

Skeletal muscles are attached to the cuticle which is often invaginated to form an apodeme at the point of attachment. Apodemes are usually short, but sometimes are long and tendon-like so that the muscle may be some distance from the skeletal element which it moves. For example, pretarsal depressor muscles occur in the femur and proximal tibia (Fig. 2.32). Large, flat apodemes provide for the insertion of large muscles such as those of the mandibular and the tibial extensor muscles of grasshoppers (Fig. 2.32).

Movement of most skeletal elements, such as a leg segment, is controlled by pairs of antagonistic muscles, one inserted on each side of the articulation (Fig. 2.6B).

Jumping, which requires the sudden exertion of great force, is produced by a relatively slow build up of tension by distortion of some part of the cuticle by a powerful muscle (Fig. 2.32). The sudden release of this tension is produced by some secondary mechanism and involves the

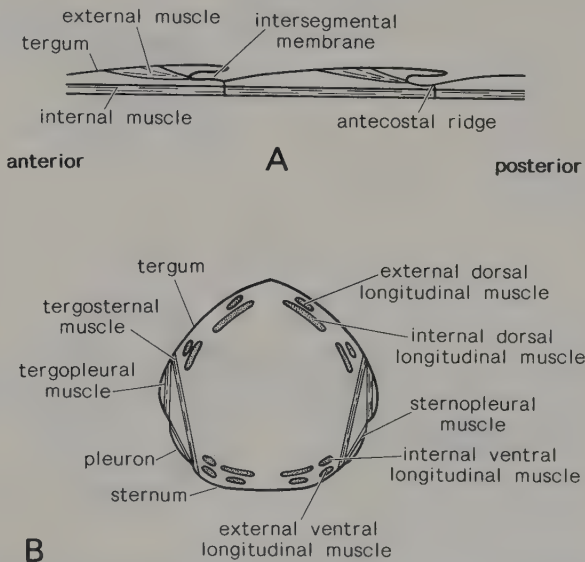


Fig. 2.31 Muscles: arrangement in an abdominal segment: A, dorsal longitudinal muscles; B, transverse section. [After Snodgrass in Chapman 1982; L. Warrenner]

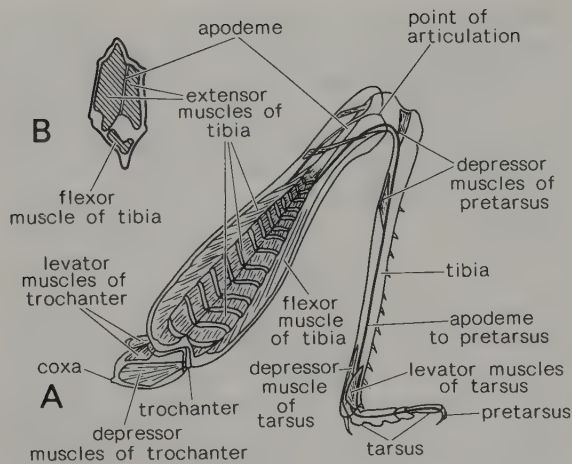


Fig. 2.32 Jumping: hind leg of grasshopper, showing arrangement of muscles and apodemes: A, outer cuticle removed; B, transverse section of femur. [After Snodgrass in Chapman 1982; A. Carter]

rapid shortening of the power muscle and the restoration of the cuticle to its normal, unstressed state. In fleas energy for the jump is stored in a pad of resilin at the base of the hind femur; in grasshoppers the distal end of the femur itself is distorted.

Flight

The muscles producing movements of the wings are usually the largest in the body, occupying much of the space in the wing-bearing segments. Some dorsoventral muscles are inserted at the wing base into the basalar and subalar

sclerites. Because they act directly on the wing, pulling it down, they are called *direct* flight muscles. In Odonata, Blattodea and Mantodea they are the only wing depressor muscles but in other orders most power for the downstroke is produced by the dorsal longitudinal muscles which run from phragma to phragma of each wing-bearing segment. The structure of the thorax is such that contraction of these muscles distorts the cuticle of the thorax, causing the tergum to bow upwards and this, because of the nature of the articulation of the wing with the thorax, produces the downstroke (Fig. 2.33). These are called *indirect* flight muscles because of their indirect mode of action.

The upstroke, levation, is produced by indirect flight muscles in all insects. These are dorsoventral muscles running from tergum to sternum or coxa. When they contract they pull down the tergum, lowering the tergal articulation of the wing relative to the pleural articulation so that the wing is raised (Figs 2.33, 34).

The wingbeat frequency is very variable and there is a general tendency for it to be higher in smaller insects. In butterflies it is usually in the range 4–20 Hz, in grasshoppers 15–30 Hz, while in flies and bees and wasps it is generally over 200 Hz. The lower wingbeat frequencies are produced by synchronous muscles, but high frequencies involve fibrillar, asynchronous muscles.

To produce the aerodynamic forces necessary to keep the insect in the air, and to permit manoeuvrability, the wings do not move straight up and down, but oscillate in a complex manner. Relative to the body of the insect, the wing tip moves in an ellipse or figure-of-eight, forward on the downstroke and back on the upstroke. In addition,

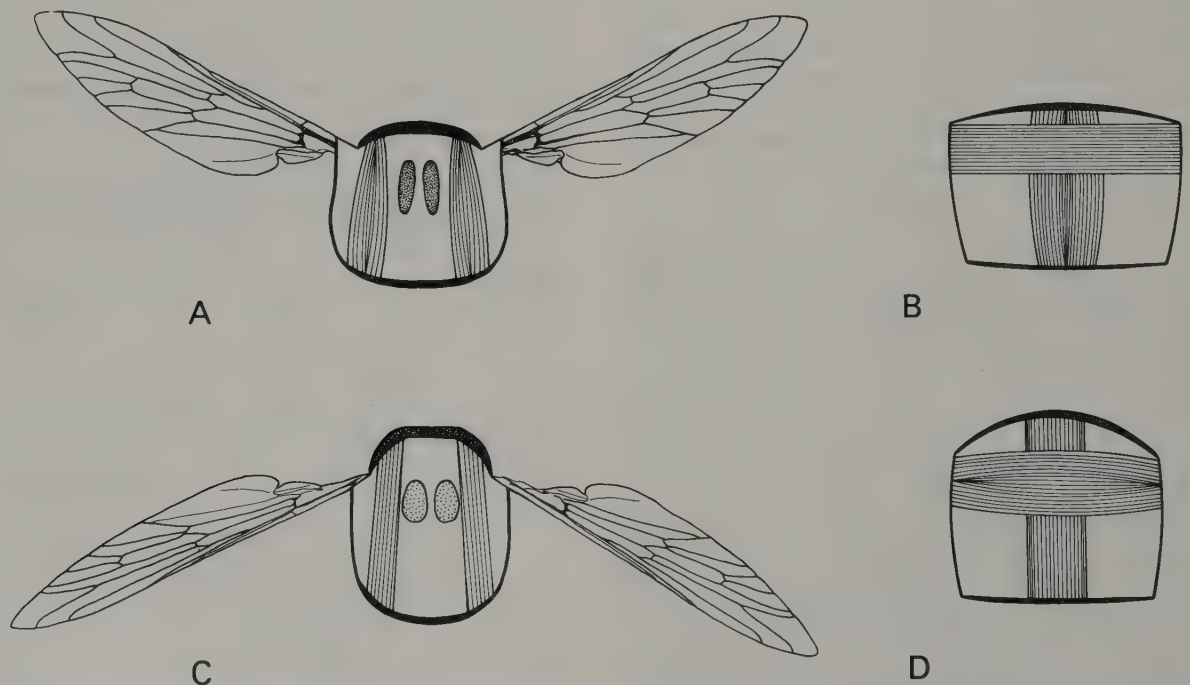


Fig. 2.33 Flight muscles: diagrams showing mode of action of indirect flight muscles: A, C, cross-sections of thorax; B, D, views of wing-bearing segment from inside. Contraction of dorsoventral muscles depresses tergum and lowers wing-tergal articulation, causing wing to go up (A, B). Contraction of dorsal longitudinal muscles forces tergum up, raising wing-tergal articulation and causing wing to go down (C, D). [After Chapman 1982; A. Hastings]

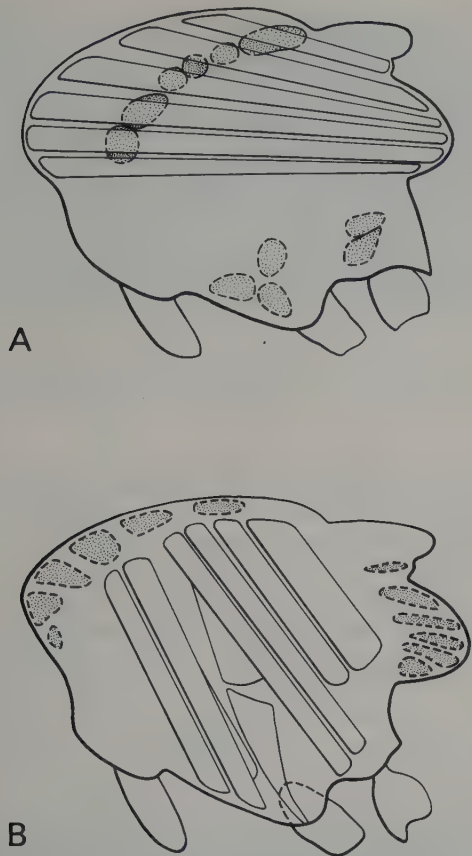


Fig. 2.34 Flight muscles: sagittal section of *Drosophila melanogaster* (DIPT), showing flight muscles. [After Miller in Kammer 1985; A. Hastings]

the plane of the wing is twisted so that, in general, the leading edge is down relative to the wing membrane on the downstroke and up on the upstroke (Fig. 2.35). This complex series of changes is produced partly by the nature of the wing articulation and partly by differential contraction of the basalar and subalar muscles. The arrangement of the veins of the wing also affects the attitude which the wing assumes during different phases of the wingstroke.

EXOCRINE GLANDS

Exocrine glands secrete material to the outside of the body, in contrast to the endocrine glands which produce internal secretions. Epidermal gland cells are basically of two types, with or without a duct leading to the outside. In the absence of a duct it is presumed that the secretion reaches the outside of the cuticle via the pore canals and epicuticular filaments.

Isolated gland cells, scattered through the epidermis, contribute to the formation of the epicuticle (Fig. 2.1); the glands of mature males of *Schistocerca* produce a pheromone which experimentally speeds up the rate of maturation of immature individuals. In most cases, however, the cells are aggregated into discrete, glandular structures. Among these exocrine glands are salivary glands and silk glands, and glands producing pheromones and defensive secretions.

Salivary Glands

The salivary glands open by a single median duct into the pre-oral cavity. The paired glands lie in the thorax or abdomen. In most insects they are acinous glands, consisting of numerous small spheres of cells connecting to the main ducts (Fig. 2.36), but in Diptera they are tubular and in plant-sucking bugs they are complex, lobed structures. Irrespective of their anatomical appearance the cells of the glands are differentiated to produce enzymes, to pass water from the haemolymph to the ducts, and to reabsorb ions from the ducts. In some insects there is a salivary reservoir.

The principal function of the glands is to produce salivary enzymes, but in plant-sucking bugs they also produce the components which form the stylet sheath formed in the plant tissues during penetration of the stylets. The salivary enzymes facilitate the ingestion of food by degrading structural components of the host tissues and by making complex molecules soluble. The enzymes present in the saliva of any species are adapted to the diet. For example, aphids possess a pectinase which disrupts the middle lamellae of plant cell walls and so aids penetration of the host tissues; the saliva of carnivorous Heteroptera contains hyaluronidase which attacks the mucopolysaccharides of connective tissue and facilitates the spread of other enzymes. Amylase is present in the saliva of many species. Protease and lipase are also often present, but not in phloem-feeding aphids and mirids. Enzymes are absent from the saliva of most haematophagous insects.

Silk Glands

In larval Lepidoptera and Trichoptera the labial glands, which are the functional salivary glands of most insects, produce silk. The silk glands are cylindrical and are often very conspicuous in the haemocoel (Fig. 2.37). The posterior part of the gland produces the silk protein, fibroin.

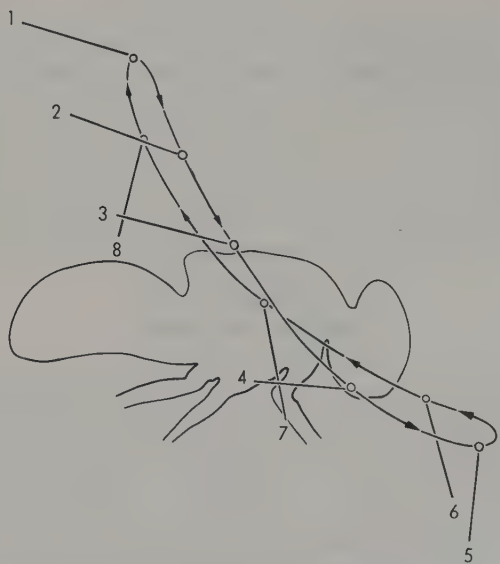


Fig. 2.35 Flight: movement of fly wing during flight, showing differences in degree of wing twisting at different points in stroke [After Chadwick in Roeder 1953]

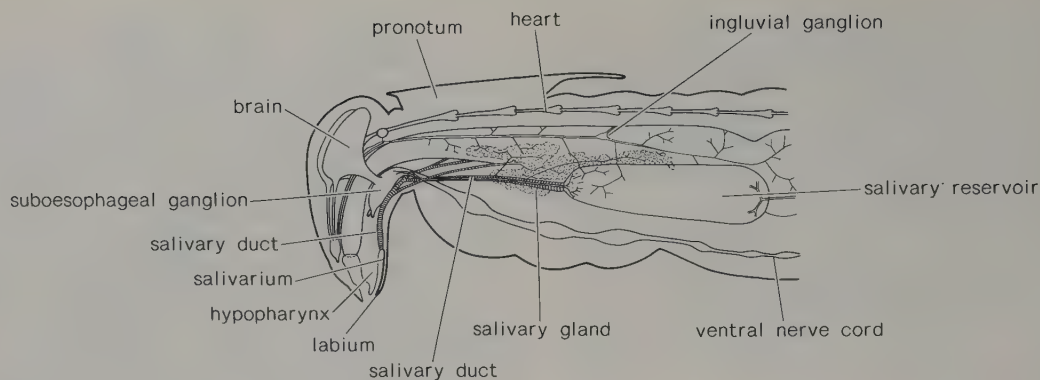
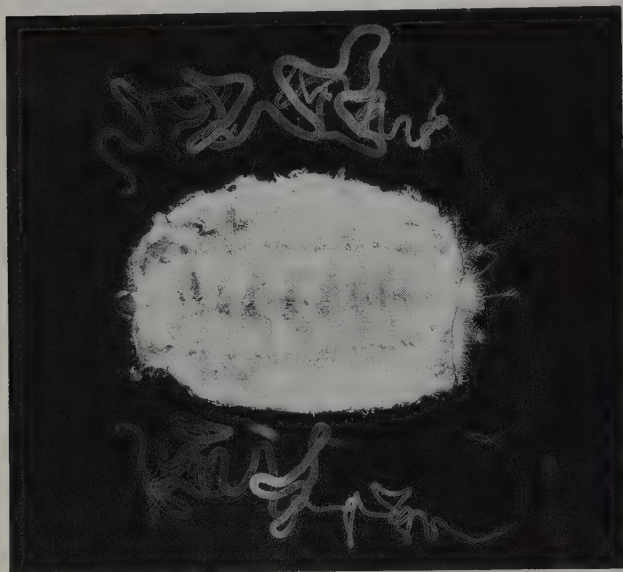


Fig. 2.36 Salivary gland and reservoir of cockroach.

[After House and Ginsborg 1985; A. Carter]

Fig. 2.37 Silk glands in larva of *Opodiphthera helena* (LEPI: Saturniidae).
[J. Green, J. P. Spradbery]

This is stored in the middle part of the gland and moulded into a thread as it is extruded. A second protein, sericin, secreted in the middle part of the gland coats the silk threads and binds them together in the cocoon. Silk is also produced from modified salivary glands in some Diptera, Hymenoptera and Psocoptera. In Neuroptera and a few Hymenoptera silk is produced in modified Malpighian tubules and in the Embioptera the glands are in the fore tarsi.

Pheromone Glands

Pheromones are substances which, if passed from one individual to another of the same species, cause the recipient to respond behaviourally or physiologically in a particular way. They are produced by glands on different parts of the body. For example, in many female Lepidoptera the glands producing the male sex attractant pheromone are beneath the intersegmental membrane of one of the posterior abdominal segments (Fig. 2.38). Termites, cockroaches and many social Hymenoptera also have abdominal pheromone glands. Nearly all

Hymenoptera have a pheromone-producing mandibular gland, the duct from which opens into a groove on the mandible. In scolytines and tephritids pheromones are produced in the hind gut.

Release of the pheromone often involves exposing the gland. In the case of abdominal glands this may be achieved by depressing the tip of the abdomen, if the gland is in a dorsal position, or by extruding the gland through haemolymph pressure. In many male Lepidoptera the glands producing aphrodisiac pheromones are associated with dispensers. Often these glands are on the wings

Fig. 2.38 Pheromone gland at base of ovipositor in *Merophyas* sp. (LEPI: Tortricidae) (scale = 50 μ m). Arrow pointing to gland.
[K. Pickerd]

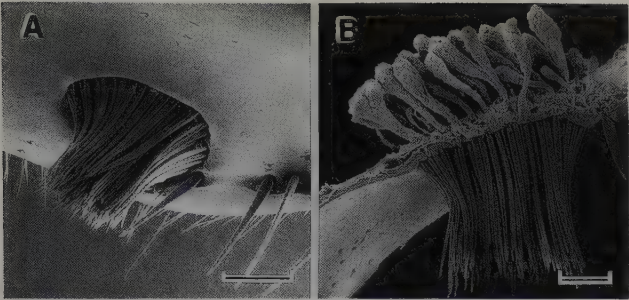


Fig. 2.39 Pheromone dispenser: A, tuft of hairs on fore trochanter of male *Onitis aygulus* (COLE: Scarabaeidae); B, section through tuft, showing large gland cells with ducts opening between hairs. Scale = 100 μ m. [After Houston 1986; C. D. Beaton]

and the dispensers may take the form of specialised scales, usually with frilled margins to enhance evaporation. In other cases elaborate structures, called hair-pencils or brushes, are normally concealed within the abdomen but are everted during courtship to dispense the pheromone. Some scarabs have at the base of the fore leg a group of hairs which probably functions in a similar way (Fig. 2.39).

Pheromones are produced and released in extremely small quantities; most estimates indicate a release rate of less than one nanogram (10^{-9} g) per minute. Many are transmitted as odours and so can be utilised as signals for affecting the behaviour of conspecifics at some distance from the insect producing them. In this category are sex attractant pheromones, produced by insects in several orders, most often by females, and alarm pheromones produced by social Hymenoptera and aphids. Other pheromones are transmitted by contact; for example the sex pheromone of the tsetse fly and queen substance of *Apis*.

A variety of chemicals are employed as pheromones. In the case of sex attractant pheromones molecular size is determined by the conflicting requirements for a high volatility, specificity and the ability of the insect to synthesise the compound. Lepidopteran sex attractants are aliphatic compounds with from 10 to 21 carbon atoms

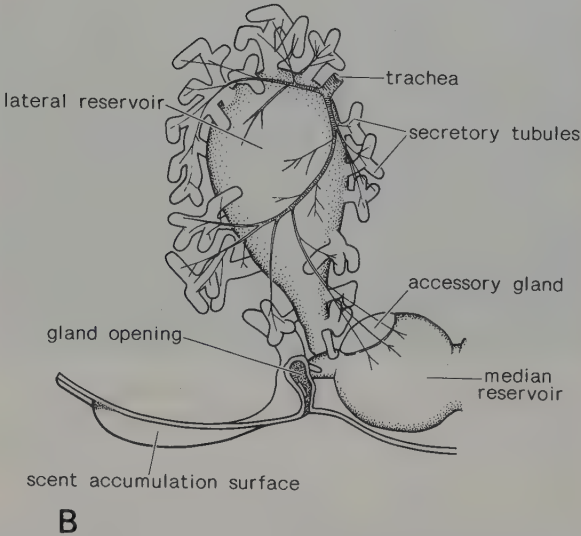
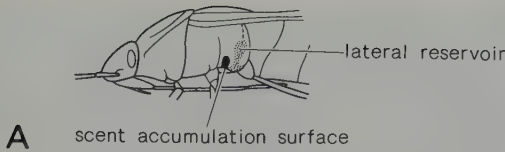


Fig. 2.40 Defence glands of *Oncopeltus* (HEMI: Lygaeidae) adult: A, side view showing position of metathoracic scent apparatus; B, diagram of scent apparatus of left side. [After Staddon 1979; A. Carter]

and molecular weights of 156 to 310. Specificity may be enhanced by the production of a mixture of compounds and it is evident that many sex attractant pheromones are multicomponent systems. Examples of some of the chemicals employed as pheromones are given in Table 2.4.

Defence Glands

Many insects produce secretions which are deterrent to potential predators or parasites. Chemicals producing these effects are sometimes called allomones—chemicals which are adaptively favourable to the producer. The

Table 2.4 Examples of chemicals used as pheromones

Function	Species	Compound
sex attractant	<i>Grapholita molesta</i> *	<i>cis</i> -8-dodecenyl acetate <i>trans</i> -8-dodecenyl acetate dodecyl alcohol <i>cis</i> -8-dodecenyl alcohol
aphrodisiac	<i>Danaus gilippus</i>	pyrrolizidine alkaloid
aggregation	<i>Dendroctonus brevicomis</i>	frontalin <i>exo</i> -brevicomin
alarm	<i>Formica</i> spp. <i>Megoura viciae</i>	formic acid α -pinene β -pinene
trail	<i>Monomorium pharaonis</i>	3-butyloctahydro-5-methylindolizine
social regulation	<i>Apis mellifera</i> *	(<i>E</i>)-9-oxo-2-decenoic acid (<i>E</i>)-9-hydroxy-2-decenoic acid

* The pheromone is a mixture of the compounds listed.

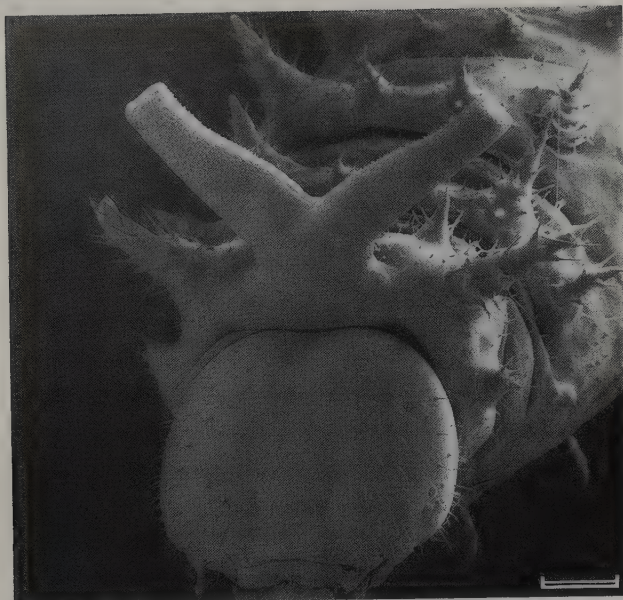


Fig. 2.41 Defence gland of larval *Papilio* (LEPI: Papilionidae): expanded osmeterium, showing complex surface from which chemicals volatilise. [C. D. Beaton]
Scale = 0.2 mm.

glands secreting these substances differ, in general, from pheromone glands in possessing a reservoir in which the defensive material is stored because the quantities of chemicals involved are much greater than those employed as pheromones. In many instances the chemicals are forcibly ejected by direct muscular compression of the reservoir or by haemolymph pressure. Examples of this type of gland are the frontal gland of termites, opening on the head, and the metathoracic and abdominal glands of many Heteroptera (Fig. 2.40).

Eversible defensive glands are described from a few species; the osmeterium of papilionid larvae is an example (Fig. 2.41). The whole structure is normally completely inverted within the body, just behind the head, but when the larva is disturbed it is everted by haemolymph pressure.

Many different classes of chemicals are used for defence. In most cases they are probably synthesised by the insects, but these substances may be toxic to the producers themselves and there is some evidence that their final production occurs extracellularly. As with some pheromones, the production of some defensive chemicals is dependent on their availability in the diet and many insects sequester plant toxins.

ALIMENTARY CANAL

The alimentary canal comprises three sections, the fore, mid and hind guts (Fig. 2.42), which differ structurally, functionally and in their origins.

Fore Gut

The fore gut is formed from an invagination, the stomodaeum, of the embryonic ectoderm and, like all ectodermal structures, it is lined by cuticle. Because this lining

is morphologically on the inside of the gut it is sometimes referred to as the intima. The anterior opening of the fore gut, the mouth, is proximal to the mouth parts (i.e. the mouth parts are *outside* the mouth and there is no equivalent of the vertebrate buccal cavity) which enclose a preoral cavity known as the cibarium. In fluid-feeding insects the cibarial muscles are strongly developed and the cibarium forms a pump, forcing fluid back into the fore gut. The first part of the fore gut proper, the pharynx, also forms a pump with a similar function, but is usually only weakly developed. Behind the pharynx is the oesophagus. This is a simple, tubular structure conducting food back to the crop and mid gut. Food is temporarily stored in the crop which may simply be a section of the fore gut which is capable of being distended by extending folds in the wall (Orthoptera), or may be a lateral diverticulum connected to the oesophagus by a narrow duct, as in adult Diptera and Lepidoptera. The cuticular lining of the crop is impermeable in most insects so that food can be stored without affecting the concentrations of solutes in the haemolymph. Sometimes, as in cockroaches and termites, the cuticle at the posterior end of the fore gut forms a series of well-sclerotised lobes which have a grinding function. This section is called the proventriculus, or gizzard.

Mid Gut

The mid gut is endodermal in origin, it does not have a cuticular lining and its circular and longitudinal muscles are poorly developed. The mid gut epithelial cells are tall and columnar, with microvilli on the surface facing the lumen. These cells are relatively short lived and are continually replaced by division of undifferentiated cells which often occur in groups (nidi) at the base of the epithelium. Consequently the principal cells of the mid gut pass through a series of phases from newly formed, through a highly active production phase indicated by extensive endoplasmic reticulum, to breakdown. All phases may occur together; their occurrence may be correlated with feeding or there may be spatial differences along the gut. Except for the reproductive cells, this is the only tissue in which mitosis is not limited to the period associated with moulting.

Some anatomical differentiation of the mid gut is often apparent. This commonly takes the form of caeca, usually at the anterior end. In many groups, e.g. Orthoptera, these probably serve mainly to increase the secretory/absorp-

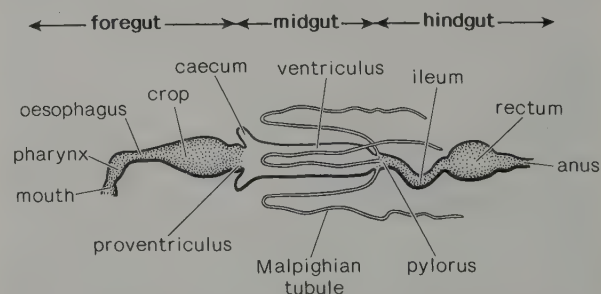


Fig. 2.42 Alimentary canal: fore gut and hind gut (shaded) are lined with cuticle; Malpighian tubules attach at the mid gut-hind gut boundary.

[After Snodgrass in Chapman 1982; A. Hastings]

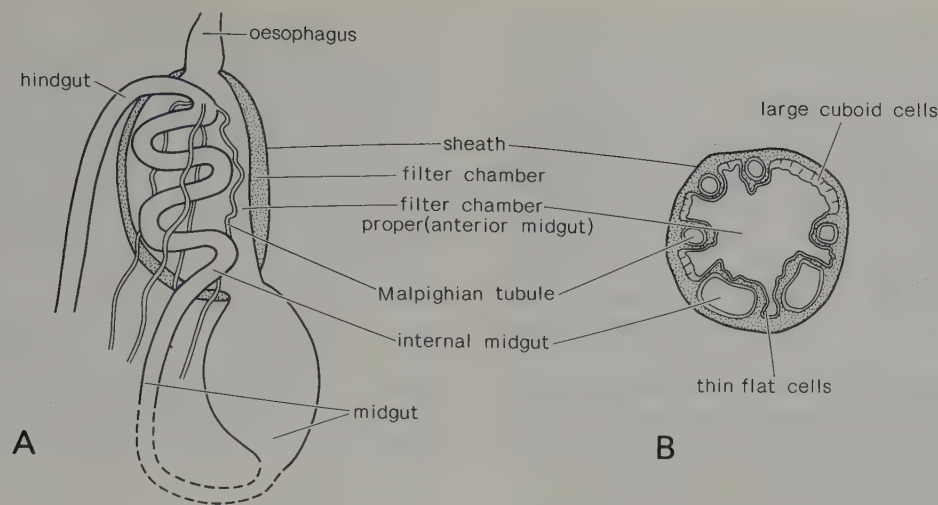


Fig. 2.43 Filter chamber of cercopid bug: A, longitudinal arrangement; B, transverse section through filter chamber. [After Marshall and Cheung in Chapman 1985; A. Carter]

tive capacity of the mid gut. In Pentatomoidea, however, where they are numerous and occur in the the posterior mid gut, the caeca contain micro-organisms.

The Auchenorrhyncha and Sternorrhyncha exhibit various modifications for eliminating excess water, the most obvious anatomical adaptation being the filter chamber of the xylem-feeding Cicadoidea (Fig. 2.43). Here the anterior mid gut forms a thin-walled bladder which wraps around the posterior mid gut and the proximal ends of the Malpighian tubules. Potassium is actively secreted into the tubules and posterior mid gut so water is drawn osmotically directly from the anterior mid gut. In this way the solutes in the xylem are concentrated, permitting more efficient absorption of nutrients, and dilution of the haemolymph is prevented.

Even where anatomical differentiation of the mid gut does not occur there may be histological or physiological differentiation. In larval Lepidoptera, for example, goblet cells which secrete potassium into the gut are abundant among the principal cells, and possible endocrine cells have been described in a number of species.

Digestion. The mid gut cells produce digestive enzymes and secrete them into the gut. The process by which they do so remains unclear. Some enzymes are secreted in vesicles released between the microvilli or by

‘blebbing’ of the microvilli. The extent to which final breakdown of the cells is associated with enzyme release is still not clear.

The types of enzyme produced are adapted to the diet (Table 2.5), and within a class of enzyme there may be many specific ones. For example there are at least seven carbohydrases in the gut of *Locusta*, each attacking a specific substrate.

Most plant-feeding insects do not digest cellulose and even among wood-feeding insects most species depend on gut symbionts (bacteria or flagellates) which digest and assimilate the cellulose, or on fungi which contribute to the complex of enzymes necessary for cellulose digestion. These adaptations are often associated with anatomical and behavioural adaptations for housing and transferring the symbionts. Larval Scarabaeoidea and termites, for example, have a hind-gut pouch in which the symbionts are housed.

Absorption. Absorption occurs in the mid gut, facilitated by the large surface area. In general it is assumed that only small molecules, such as monosaccharides and amino acids, are absorbed, although it is known in a few cases that proteins are taken into the cells. The mid gut cells of *Rhodnius*, for example, are known to absorb haemoglobin unchanged.

Table 2.5 Mid gut enzymes secreted by insects with different diets (* indicates presence of enzyme; data from Wigglesworth 1965)

Insect	Diet	Protease	Lipase	Amylase	Invertase	Maltase
Cockroach	omnivorous	*	*	*	*	*
<i>Carausius</i>	phytophagous	*	*	*	*	*
Lepidoptera						
larvae	phytophagous	*	*	*	*	*
adults	nectar	—	—	—	*	—
adults	non-feeding	—	—	—	—	—
<i>Lucilia</i>						
larvae	meat	*	*	—	—	—
<i>Calliphora</i>						
adults	sugars	weak	—	*	*	*
<i>Glossina</i>	blood	*	?	weak	—	—

Many substances are absorbed passively along a concentration gradient. This demands the maintenance of a high concentration of the substance in the mid gut lumen and a relatively low concentration in the haemolymph. The high mid gut concentration is achieved at least partly by absorbing water, while the low haemolymph concentration involves metabolising the substance in the fat body adjacent to the gut. Glucose, for example, is rapidly converted to trehalose so that its concentration in the haemolymph is always relatively low. Some specific amino acids and other substances are probably absorbed actively.

Peritrophic membrane. In many insects the mid gut is lined, at least temporarily, by a delicate, perforated membrane, the peritrophic membrane (Fig. 2.44). This may be produced in sheets by all the mid gut cells so that successive, concentric layers are present in the lumen, or by a ring of cells at the anterior end of the mid gut. The former type generally occurs in Odonata, Orthoptera, Coleoptera and Hymenoptera; the latter in Diptera. In mosquitoes and grasshoppers it is known that the membrane is produced immediately after feeding, and in the larva of *Bombyx mori* at least one enzyme is secreted bound to the membrane in an inactive form, subsequently being released into the gut lumen. One function of the peritrophic membrane may be to transport enzymes into the lumen. It may also help to conserve enzymes by permitting a differential flow of fluids within and outside the membrane. In Acrididae its thickness is correlated with the ability of the insects to consume plants containing tannins; the tannins become adsorbed on to the membrane and are subsequently voided with the faeces. It may also have a purely mechanical effect, protecting the mid gut cells from abrasion; a more conspicuous peritrophic membrane is usually present in insects eating solid food compared with fluid feeders.

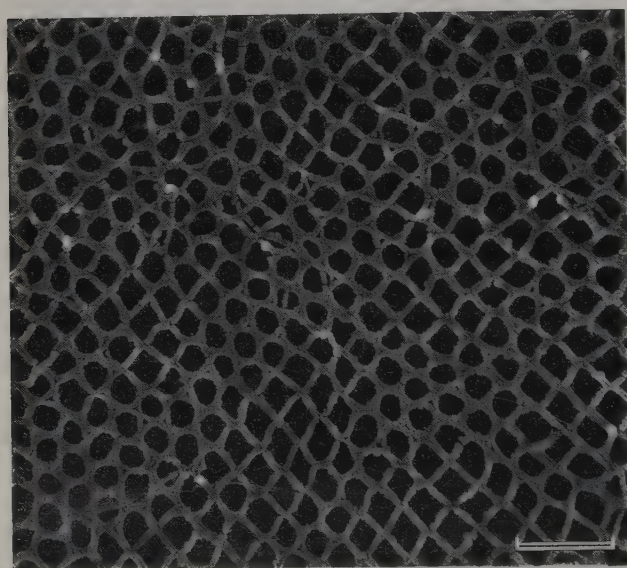


Fig. 2.44 Peritrophic membrane of *Periplaneta americana* (BLAT: Blattidae), washed in distilled water to remove amorphous material. Scale = 0.5 μ m. [C. D. Beaton]

Nutrition

The metabolic requirements of insects are basically the same as those of other animals with the same requirements for amino acids and vitamins. Most of these needs are met by the diet, but in some cases a specialised diet does not provide all the components and these are then produced metabolically or, in some cases, by symbiotic micro-organisms.

Carbohydrates are the main source of energy in most insects and are a dietary requirement, although in some cases lipids can provide an alternative source. Whether or not a carbohydrate has nutritive value for an insect depends on the enzymes available to digest it, and so facilitate absorption, and the ability of the insect to metabolise the resulting monosaccharides. Hexose sugars are readily utilised whereas pentose sugars and sugar alcohols usually are not.

Insects have no bulk requirement for lipid in the diet, although lipids can be utilised in energy-producing metabolism and in some cases, as with the wax moth, growth is optimal when lipids are the primary energy sources. However most insects do have a dietary need for polyunsaturated fatty acids such as linoleic or linolenic acid. Without these the insects fail to moult properly.

Insects cannot synthesise sterols or carotenoids. Sterols are constituents of lipoproteins and of the moulting hormone, ecdysone. Vitamin A is a carotenoid from which the visual pigment is derived. Such compounds are essential in the diet or may be supplied by micro-organisms. In some cases sufficient material may be stored by one stage for a subsequent stage to develop in its absence and so apparently to lack a requirement for that substance. For that reason it is important for nutritional studies to be continued for long enough to ensure that the results are not influenced by storage.

The conversion of one amino acid to another by transfer of an amino group, a process known as transamination, is widespread in insects; glutamic acid is of particular importance in these reactions. However insects cannot synthesise the aromatic ring which constitutes the basic skeleton of tyrosine or phenylalanine. Tyrosine has an essential role in tanning the cuticle because acetyl-dopamine is derived from it. Consequently either tyrosine or phenylalanine, which can be converted to it, are essential dietary constituents. A dietary source of methionine is also usually essential because of the insect's inability to synthesise a sulphur-containing amino acid. Cystine and cysteine, however, can be derived from methionine. The other essential amino acids are the same as for mammals: arginine, lysine, leucine, isoleucine, tryptophan, histidine, valine and threonine.

Micro-organisms

The most commonly occurring symbiotic micro-organisms in insects are bacteria or bacterium-like forms which are found in cockroaches, termites, bugs and other insects. Flagellates are found in wood-eating cockroaches and termites, yeasts in some beetles and bugs and an actinomycete in the blood-sucking bug *Rhodnius*.

In some cases the symbionts are free in the gut lumen,

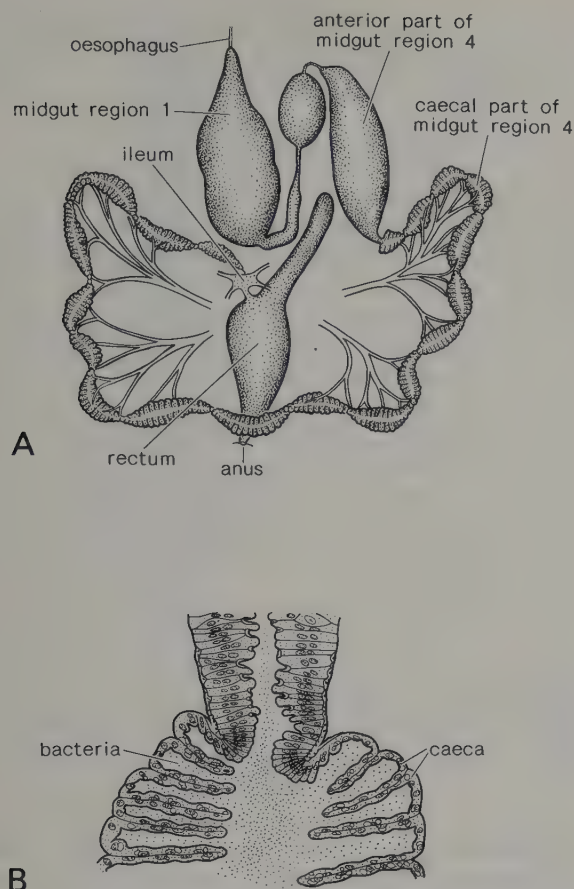


Fig. 2.45 Micro-organisms: A, alimentary canal of *Acanthocoris* (HEMI: Coreidae), showing large number of caeca in fourth region of mid gut; B, section through anterior part of caecal region.

[After Goodchild 1963; A. Hastings]

but often they occur in specialised cells, mycetocytes, or organs, mycetomes. The flagellates of termites are in the hind gut, and bacteria live in the mid gut caeca of plant-sucking Heteroptera (Fig. 2.45). Intracellular symbionts in mycetocytes are most commonly present in the fat body, while mycetomes may be associated with the gut or occupy various other positions in the body.

Internal symbiotic micro-organisms occur in insects feeding on wood, hair and feathers, vertebrate blood and plant fluids, diets which are deficient in certain, essential components or which the insect is unable to digest unaided. In most cases the micro-organisms are assumed to contribute essential nutrients which are lacking in the diet. The flagellates of cockroaches and termites contribute to cellulose digestion.

Some insects have symbionts living external to the body, but the relationship is as close as with internal symbionts. Termites of the family Termitidae depend on a fungus for their development, possibly to produce enzymes involved in the digestion of cellulose. These fungi are grown in specialised gardens in the nest and female termites exhibit specialised behaviour which ensures that they are carrying the fungus when they leave the parent nest on their nuptial flight. Comparable dependence on specific, externally growing fungi is exhibited

by ambrosia beetles and wood wasps, both of which have anatomical structures for transmitting the fungus.

Hind Gut

The hind gut, like the fore gut, is formed from an ectodermal invagination and has a cuticular intima. It is divided into a tubular section, the ileum, and a more sac-like rectum opening externally at the anus. The Malpighian tubules arise at the junction of mid gut and hind gut.

The cells of the ileum are cuboidal, but its general function is unknown.

In the rectum the epithelium is thin walled except for a number of regions, usually six, in which the cells are columnar. These regions are called rectal pads. In terrestrial insects the lateral and basal plasma membranes of the pad cells are deeply invaginated and closely associated with large numbers of mitochondria. Potassium is actively pumped into the intercellular spaces of the folds creating an osmotic gradient from the rectal lumen across the cells to the spaces. The folding is most extensive in insects from arid habitats or with dry foods, and it provides the anatomical basis for the removal (conservation) of water from the faeces. Absorption of salts, sugars and amino acids also occurs in the rectum so that nutritionally useful substances which move passively into the urine in the Malpighian tubules are recovered. Nitrogenous waste substances and potentially toxic compounds remain in the faeces. Thus the Malpighian tubules and rectum act as a complementary system, the first ensuring the removal of any potentially harmful substances from the haemolymph, the second recovering useful substances which would otherwise be lost. This system enables the insect to tolerate a wide range of potentially harmful compounds which it may not previously have encountered.

Caterpillars and some Coleoptera (e.g. *Tenebrio*) have the distal ends of the Malpighian tubules closely associated with the rectum, the whole complex of rectum and tubules being enclosed within a membrane. This cryptonephric (cryptonephridial) arrangement is concerned with improving water uptake from the rectum in *Tenebrio*; in caterpillars it may be primarily concerned with ionic regulation.

FAT BODY

The fat body is seen as irregular yellow or white tissue lying in the haemocoel. Commonly a layer of fat-body cells is closely associated with the gut and another lies close to the epidermis, but the arrangement varies from species to species and with the stage of development of the insect. The fat body comprises sheets or ribbons of cells with extensive, extracellular spaces between them through which the haemolymph percolates. Most of the cells are of one type, called trophocytes or adipocytes.

The trophocytes have a key role in intermediary metabolism. Haemolymph proteins, such as those concerned with amino acid storage before metamorphosis and the vitellogenins for yolk formation, are produced in the fat body. So is trehalose, the major circulatory carbohydrate of insects.

In addition to their synthetic role, the trophocytes store nutrients. Lipids are stored as droplets, usually of triglyceride, and carbohydrate as granules of glycogen. Protein is also sometimes stored in a granular form although usually it is released into the haemolymph. Stores of lipid and carbohydrate, and to a lesser extent protein, are built up before non-feeding periods or when the nutrient demand is likely to exceed intake. For example, the amount of stored material increases before metamorphosis and before diapause, declining during the times when the tissues are being reconstructed and the insect does not feed. The visible changes in the extent of the fat body are a reflection of these changes in the amounts of stored material.

In many insects uric acid is stored temporarily in the fat body in cells called urocytes. In cockroaches and many Hemiptera, mycetocytes, containing bacteria or bacterium-like organisms, are scattered through the fat body.

Light Production

A relatively small number of insects are luminescent. The best known are the glow-worms and fireflies, belonging to the families Lampyridae, Elateridae and Phengodidae, and a few fly larvae in the family Mycetophilidae.

In the beetles, the light-producing organs occur primarily in the abdomen and are derived from the fat body. Luminescence may occur in both sexes or be restricted to the female; it also occurs in some larval forms. Each light organ consists of a layer of light-producing cells, photocytes, beneath transparent cuticle and backed internally by a layer of cells which may form a reflecting layer. Each photocyte has a rich tracheal supply and is packed with granules, which it is presumed contain the light-producing reactants (Fig. 2.46). Light production is controlled neurally. Fireflies produce flashes of a duration and frequency characteristic of the species. The apterous females of Lampyridae produce a sustained glow. Light is emitted over a relatively narrow band of wavelengths and is generally yellow-green in colour, about 500–650 nm.

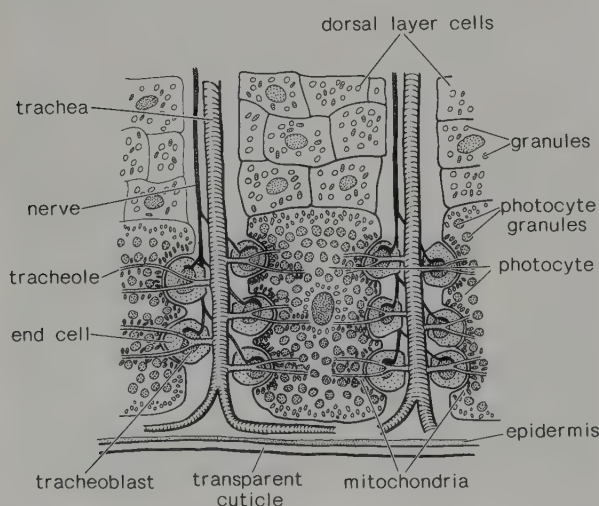


Fig. 2.46 Light producing organ of *Photuris* (COLE: Lampyridae).
[After Smith in Chapman 1982; A. Hastings]

In a few larval Mycetophilidae the light organs are derived from the enlarged, distal ends of the Malpighian tubules. The light acts as a lure for their prey.

MALPIGHIAN TUBULES

The Malpighian tubules arise at the junction of the mid gut with the hind gut (Fig. 2.42). They are long, slender, blindly ending tubes lying freely in the haemolymph and are found in all insects except Collembola and aphids. They vary in number from two in coccids to over 200 in large grasshoppers. The walls of the tubules are composed of a single layer of cells with microvilli extending into the lumen. In life the tubules are probably in continuous writhing motion in the haemolymph due to the action of muscles at their points of origin from the gut or of muscle strands running along their lengths. The effect of this movement is to prevent the persistence of local concentration differences in the haemolymph contents adjacent to the tubules.

The Malpighian tubules have a homeostatic function. Solutes in the haemolymph, including nitrogenous waste substances, pass into the tubules and from here to the hind gut from whence they are excreted. The movement of most solutes from haemolymph to tubule lumen results from the active pumping of potassium into the lumen. This creates an osmotic gradient so that water is also drawn in and other molecules then diffuse down a concentration gradient into the tubule. Consequently the fluid in the lumen of the Malpighian tubule, the primary urine, contains all the solutes present in the haemolymph but in different concentrations because their rates of diffusion vary inversely with the size of the molecule. The production of primary urine is a continuous process and the movement of water into the tubules produces a flow of urine towards and into the gut. In the hind gut, and especially in the rectum, selective resorption of ions and of water occurs so that the insect conserves the useful components and excretes the others. At least in some insects there are also active mechanisms for moving alkaloids and other potential toxins rapidly from the haemolymph.

Uric acid is the principal end product of nitrogen metabolism in insects. Because of its low solubility it requires little water for its safe elimination and it can even be stored in solid form in the fat body. Compared with ammonia and urea it has a higher N:H ratio so that less water is required for its synthesis (since the hydrogen is ultimately derived from water). Aquatic insects, with no shortage of water, often excrete ammonia.

CIRCULATORY SYSTEM AND HAEMOLYMPH

Circulatory System

The body cavity of insects is a haemocoel and organs such as the alimentary canal, Malpighian tubules and muscles are bathed directly by the blood. The nervous system is isolated by the blood-brain barrier.

The principal circulatory organ, the heart, is a slender tube in the dorsal midline of the abdomen, sometimes extending into the thorax. Laterally its walls are perfora-

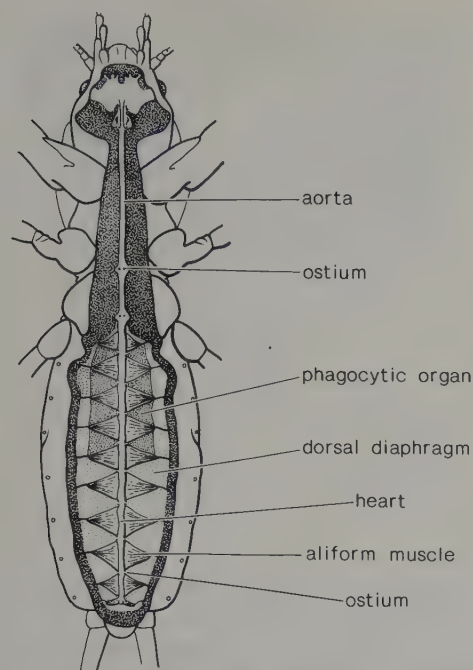


Fig. 2.47 Circulatory system: ventral dissection of *Gryllotalpa* (ORTH: Gryllotalpidae), showing dorsal vessel. Dorsal diaphragm is continuous over the ventral wall of the heart, but is omitted in the diagram.

[After Nutting in Chapman 1982; A. Hastings]

ted by paired, valved ostia and anteriorly it extends to the head as the aorta which opens into the haemocoel in front of and beneath the brain. The heart is supported by wing-like aliform muscles in the abdominal segments and lies in a dorsal segment of the haemocoel above a fenestrated dorsal diaphragm (Fig. 2.47). In some insects the heart is innervated by a series of neurons situated along its length with their axons forming lateral cardiac nerves. These may be joined by segmental nerves originating in the segmental ganglia of the ventral nerve cord, while in other instances only the segmental nerves are known to be present. In some species, *Anopheles* for example, the heart apparently is not innervated.

Other circulatory organs occur in other parts of the body. In most insects a muscular diaphragm exists above the ventral nerve cord and accessory pulsatile organs may pump blood into the antennae, legs and, perhaps, the wings. The cavities of the legs and antennae of at least some insects are divided by a longitudinal septum which is presumed to act, together with the basal pulsatile organ, in directing a flow of blood into the appendage along one compartment and out from it along the other.

Blood passes into the heart via the ostia and is pumped forwards by contraction of the heart muscles, passing out of the aorta into the haemocoel in the head. From here it flows backwards, drawn by the systolic activity of the heart and assisted by rhythmic movements of the ventral diaphragm.

Structure of Blood

The blood, or haemolymph, contains many chemicals in solution. The major inorganic ions are sodium, potassium,

calcium and magnesium, chloride, phosphate and bicarbonate. Trehalose is the principal blood sugar. Another characteristic feature of insect haemolymph is its high amino acid content. A number of proteins are also present.

Several types of blood cells are present in the haemolymph. These are all nucleate and vary in form from small, round cells with relatively little cytoplasm (prohaemocytes), to large basophilic cells with irregular outlines (plasmatocytes) and others in which the cytoplasm is characteristically granular (granulocytes). Various other types have been described.

Also within the haemocoel, but ensheathed in basement membrane, are cells called nephrocytes. They are probably present in all insects and occur, singly or in groups, along the side of the heart and aorta (these are often called pericardial cells) and beneath the oesophagus. Sometimes they form conspicuous chains of cells; such a chain is present between the salivary glands of blowfly larvae. Nephrocytes complement the haemocytes, fat body and Malpighian tubules in regulating haemolymph composition.

Oenocytes are also sometimes found in clusters in the haemocoel. This is true in Lepidoptera and Orthoptera. In Sternorrhyncha, Auchenorrhyncha, Hymenoptera and some Diptera they are embedded in the fat body, while in Ephemeroptera, Odonata and Heteroptera they lie between the bases of the epidermal cells and the basement membrane. They are often large cells, more than 100 μm in diameter, and relatively few in number. They show cycles of development which, in immature insects, are associated with the moulting cycle. Their functions are not certainly known, but probably include synthesis of epicuticular lipoproteins, wax and, possibly, ecdysteroids.

Functions of Blood

The principal functions of the haemolymph are as a transport medium, as a storage reservoir, to provide immunity against parasites and disease, and, in some cases, to act as a skeletal element and in thermoregulation.

Many substances are transported in solution in the haemolymph. Nutrients absorbed from the gut are carried to the tissues, and especially the fat body where much intermediate metabolism occurs. Reserves of lipid and carbohydrate are carried from the fat body to the active tissues, and nitrogenous waste is carried to the Malpighian tubules. Hormones are transported from their release sites to the target organs and the position and arrangement of the neurohaemal organs is such as to facilitate this (see p. 50). Chemicals can be transported to the extremities of the appendages within minutes of entering the haemolymph, but it may take hours for an injected marker to become uniformly distributed through the haemolymph. In insects the blood does not, in general, have a respiratory function because oxygen is carried direct to the tissues by the tracheal system; consequently no respiratory pigment is present in the blood of most insects, although haemoglobin is found in a few exceptional cases.

In a number of insects it is known that specific proteins

accumulate in the haemolymph before metamorphosis. For example, the larva of *Calliphora* synthesises a protein, calliphorin, which accumulates in the haemolymph and, in the late larva, comprises about 75% of the total haemolymph protein. During metamorphosis this protein is utilised as a source of amino acids for the synthesis of other proteins. Storage as a protein, rather than as amino acids, minimises effects on haemolymph osmotic pressure. Amino acid concentrations do, nevertheless, vary during development. The concentration of tyrosine, for example, increases before ecdysis prior to tanning the new cuticle.

The haemocytes have a major role in insect immune responses. Micro-organisms are phagocytosed, primarily by plasmatocytes and granulocytes, while larger organisms, such as parasites, are encapsulated by the accumulation of plasmatocytes round the foreign body. The inner layers of cells, adjacent to the invader, become flattened and necrotic. In addition to these cellular responses prophenoloxidase and lectins are present in the haemolymph of at least some insects and there is some evidence that these have an antimicrobial action. Other proteins, with antibacterial activity, are known to be induced following infection.

The skeletal importance of haemolymph is obvious in soft-bodied larvae of holometabolous insects in which support and movement depend on its hydrostatic skeletal function. Ecdysis and subsequent expansion of the new cuticle also require a high haemolymph volume and in the period just before ecdysis haemolymph volume increases. This is often obvious in hemimetabolous insects by the extension of flexible areas of cuticle, for example, causing the abdomen to extend and the wing pads of grasshoppers to stand away from the body. Insects which cannot achieve a high blood volume at this time often fail to complete the moult successfully.

REPRODUCTIVE SYSTEM

In both sexes the reproductive organs consist of paired gonads connecting to paired lateral ducts which join to form a single, median duct opening at the gonopore.

Male System

Each testis consists of a series of testis follicles, varying in number from one in Adephaga to over 100 in Acrididae. The paired ducts with which the follicles connect are called vasa deferentia (singular vas deferens) which join to form the ejaculatory duct. In most insects accessory glands open into the ducts and, in addition, a storage organ for sperm, the seminal vesicle, may be present (Fig. 2.48).

At the distal end of each testis follicle is the germarium in which the germ cells divide to produce spermatogonia. More spermatogonia are produced as differentiation of the older ones proceeds through spermatids to spermatozoa. Successive stages are present in sequence along the follicle with the most mature nearest the junction of the follicle with the vas deferens. Meiosis occurs in the course of this development.

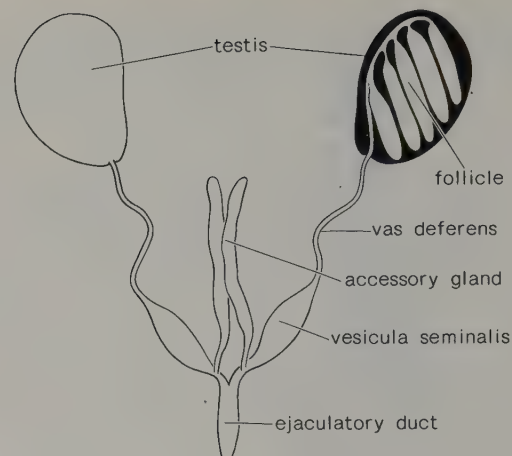


Fig. 2.48 Male reproductive system: generalised diagram.

The sperm of most insects are filamentous, often about 300 μm long and less than one micrometre in diameter. The nucleus is present at the head end, behind an attachment organ, while the 'tail' has a cilium-like arrangement of tubules associated with structures derived from mitochondria.

The secretions of the accessory glands are involved in sperm transfer. As well as forming the spermatophore, they contribute to the seminal fluid facilitating the survival of the sperm within the female. There is also increasing evidence that certain components of the seminal fluid influence the behaviour and physiology of the female.

Female System

Each ovary consists of a series of ovarioles which connect separately with the lateral oviducts. The median oviduct opens externally to a genital chamber which is sometimes invaginated to form a separate chamber (vagina) to which sperm are initially passed by the male. In addition there is a spermatheca, usually only one, in which sperm are stored after insemination. Some female insects also have accessory glands (Fig. 2.49).

Oocytes are produced in the ovarioles by division of the germ cells and oocytes in progressively later stages of development are often present in a linear series, with the oldest stages nearest the oviducts. The development of the oocytes (oogenesis) first involves mitosis, and growth by deposition of yolk (vitellogenesis). In Odonata, Orthoptera, Isoptera and Siphonaptera, there are no specialised nurse cells and such ovarioles are termed panoistic. Yolk is derived directly from substances in the haemolymph. In other groups some oogonia develop into oocytes, but others (trophocytes) have a nutritive role, contributing to the development of the oocytes. In Heteroptera and many Polyphaga the nutritive cells are concentrated in the germarial region of the ovarioles and as the oocytes move towards the oviduct they remain connected to the trophic region by a cytoplasmic cord. These are called telotrophic (or acrotrophic) ovarioles. In Dermaptera, lice and most holometabolous insects each oocyte retains cytoplasmic

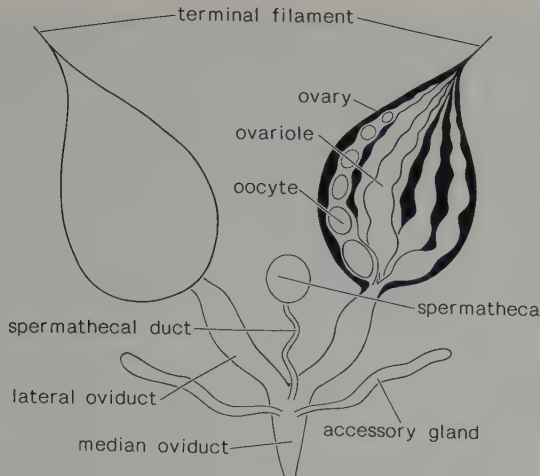


Fig. 2.49 Female reproductive system: generalised diagram.

continuity with a group of trophocytes which move down the ovariole with it. Consequently in many of these insects the oocytes appear to be bilobed in the earlier stages of development. Ultimately the trophic cells become depleted of nutrients and degenerate. These are called polytrophic ovarioles.

Each oocyte, in all types of ovariole, is clothed in a layer of cells forming the follicular epithelium, which has a function in vitellogenesis and finally secretes the egg shell, or chorion. When the egg leaves the ovariole and moves into the oviduct, a process known as ovulation, the remnants of the follicular epithelium remain in the ovariole. In some insects, at least, these remnants make it possible to determine whether oviposition has already occurred in an insect of unknown status.

In some insects fully-developed oocytes are already present at the time of the final moult, but in many cases only early oocytes are present at this time. Vitellogenesis and chorion formation then occur after a period of somatic growth in which the flight muscles increase in size and functional efficiency, and further cuticle deposition and differentiation occur. Consequently it is necessary in insects to distinguish becoming adult from becoming sexually mature; in other animals becoming adult implies sexual maturity.

Transfer of Sperm

The transfer of sperm to the female often involves a specialised structure, the spermatophore, which is produced from secretions of the male accessory glands. Within this structure the sperm are packaged so that they are protected during their transfer to the female. In some Collembola and Diplura the spermatophores are produced independently of the female and they are deposited in situations where females are likely to encounter them. In other insects sperm transfer involves the interaction of the male with the female and, except in Thysanura, male and female become coupled by the genitalia. Male gryllids and blattids produce a spermatophore which is transferred directly to the female, but which remains external to the female gonopore. In other cases the spermatophore is

formed at least partly within the female ducts, sometimes serving as a temporary extension of the male penis so that sperm are deposited directly in the spermatheca. In some Heteroptera, Hymenoptera, Coleoptera and Diptera no spermatophore is produced. Sperm are transferred directly to the female ducts, and often into the spermatheca, by the penis.

Mating and oviposition are separate in time. During the interval between these processes sperm are stored in the spermatheca, and in social insects it is evident that they may live for many months; survival for a period of weeks is probably common. The sperm remain in the spermatheca until the eggs are laid. At this time a few sperm are released as each egg moves down the oviduct past the opening of the spermathecal duct. Sperm enter the egg through the micropyles in the chorion. Hence it is important to distinguish between *insemination* of the female and *fertilisation* of the egg.

DEVELOPMENT

Egg

Insect eggs are large relative to the size of adult insects because of the large amount of yolk they contain. They are commonly globular, conical or sausage-shaped in form, but the eggs of some Diptera and Nepidae have respiratory horns while those of Chrysopidae are stalked (Fig. 2.50). The egg shell, or chorion, is a complex structure chemically and architecturally. It is formed entirely by the follicle cells in most species and is often sculptured with a basically hexagonal pattern, reflecting the outlines of these cells. Sperm entry to the egg occurs through a funnel-shaped canal, the micropyle, which passes right through the chorion (Fig. 2.51). In most Diptera the egg has only a single terminal micropyle, while Acrididae commonly have 30 to 40 arranged in a ring round one end. In Pentatomomorpha the micropyles open on small cup-shaped processes.

Most insect eggs have a series of air-filled cavities in the inner layers of the chorion which connect with the outside air through a series of openings, the aeropyles. In *Rhodnius* there is a ring of aeropyles just below the cap, while in *Musca* they are distributed over the whole surface of the egg. Sometimes, as in *Drosophila*, the openings are restricted to respiratory horns. This arrangement facilitates respiration while minimising water loss. The chorion lining the openings has hydrofuge properties so that water does not enter the airspaces if the eggs become submerged in water; in some species the air-water interface formed in these conditions is large enough to function as an efficient plastron. This is true of the eggs of many Diptera (Fig. 2.52). Eggs which are laid in water, such as those of dragonflies, obtain their oxygen from that dissolved in the water.

The chorion itself is not waterproof in most insects. Water loss may be limited by a layer of wax on the inside of the chorion or, in Orthoptera, associated with the serosal cuticle, produced on the outside of the egg early in embryonic development.

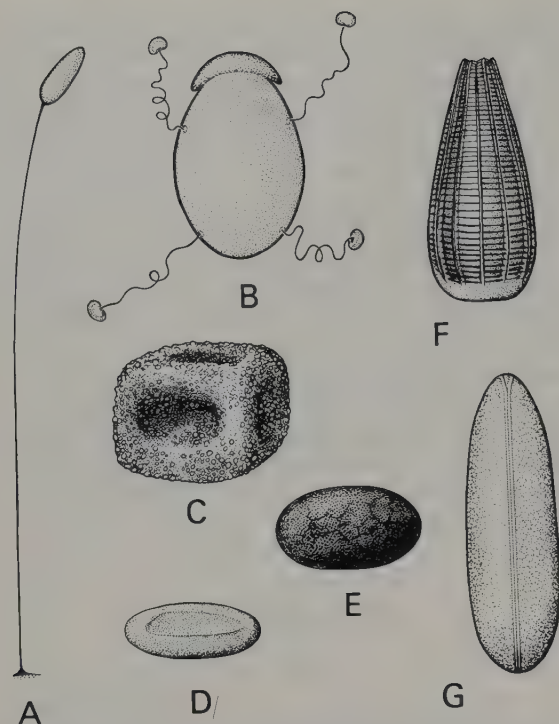


Fig. 2.50 Eggs: A, Chrysopidae (NEUR) (stalk about 5 mm); B, Baetidae (EPHE) (0.18 mm X 0.09 mm); C, *Harpobittacus* (MECO: Bittacidae) (0.8 mm X 0.6 mm); D, *Stenoperla* (PLEC: Eustheniidae) (0.3 mm X 0.1 mm); E, *Coscinocera* (LEPI: Saturniidae) (3.5 mm X 2 mm); F, *Pieris* (LEPI: Pieridae) (height about 2 mm); G, *Lucilia* (DIPT: Calliphoridae) (1.0 mm X 0.3 mm). [S. Monteith]

Embryology

Embryonic development begins immediately following oviposition and fertilisation, although in some species an embryonic diapause occurs relatively early in development. The first stage is the formation of a layer of cells, the blastoderm, over the outside of the egg and completely enclosing the yolk. Part of this layer becomes thickened to form the germ band, the rest of the blastoderm remaining as extraembryonic ectoderm. The extent of the germ band varies: in Exopterygota it consists initially only of a cap or strip of cells at one end of the egg, whereas in Diptera the germ band occupies most of the blastoderm from the outset and presumptive larval areas are already distinguishable at this time. Subsequently the embryo becomes two-layered. From the outer layer are derived all the ectodermal structures of the insect including the fore and hind guts and the tracheal system which form from invaginations. The nervous system also has an ectodermal origin. From the inner layer mesodermal structures are formed: muscles, heart and reproductive ducts. The mid gut forms from groups of cells at either end of the inner layer.

The developing germ band does not usually remain on the surface of the egg, but is temporarily covered by one or more embryonic membranes. These disappear as the embryo grows and its ectodermal layer extends so that it encloses all the yolk. In most insects the enclosure of the yolk involves a series of movements of the embryo during which it may completely reverse its position in the egg.

The movements are most marked in Odonata and Tettigonioidae whereas in Diptera no movements occur. The movements are known collectively as blastokinesis.

As the embryo grows it becomes segmented and at some stages the mandibular, maxillary and labial segments are recognisable as distinct post oral segments with paired appendages which are clearly homologous with the legs. Eleven segments may also be recognisable in the abdomen and here, too, rudimentary appendages are present although, except for the genitalia, they do not persist.

The germ cells, which ultimately produce the sperm and oocytes in the adult insect, are recognisable at a relatively early stage of development and in Diptera, Coleoptera and Hymenoptera they are differentiated at the very start. Consequently there is a very direct cell lineage from the gametes of one generation to those of the next in isolation from the structural cells of the body.

Hatching

The fully developed larva escapes from the egg (hatches) by rupturing the chorion. This involves swallowing the fluids in which the larva is bathed within the egg and any air which has entered, and then pumping blood forwards by contractions of the abdomen so that the head exerts

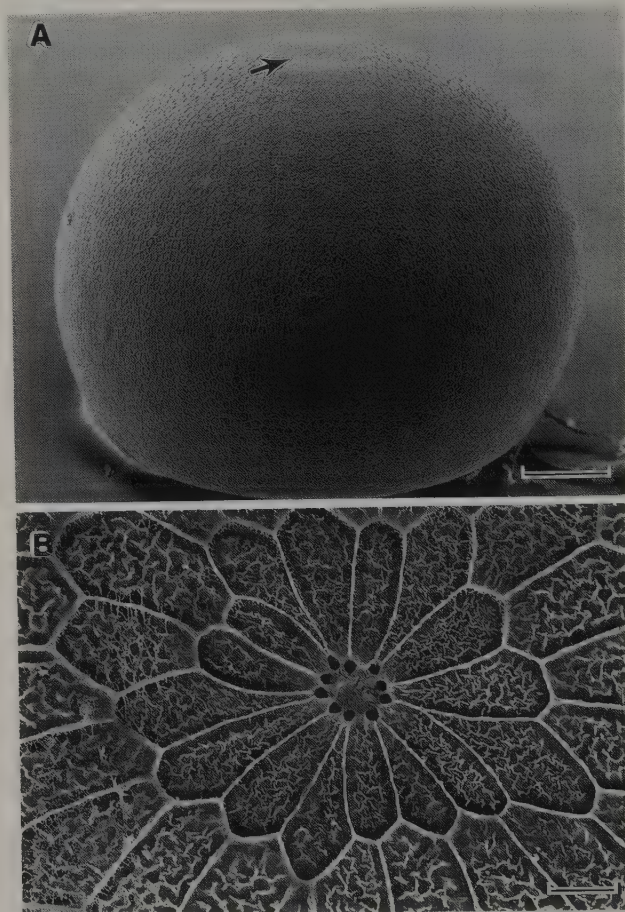


Fig. 2.51 Egg of *Neola semiaurata* (LEPI: Noctuidae): A, whole egg (arrow pointing to micropyle; scale = 0.2 mm); B, micropyles on dorsal surface (scale = 10 μ m). [E. Brooks]

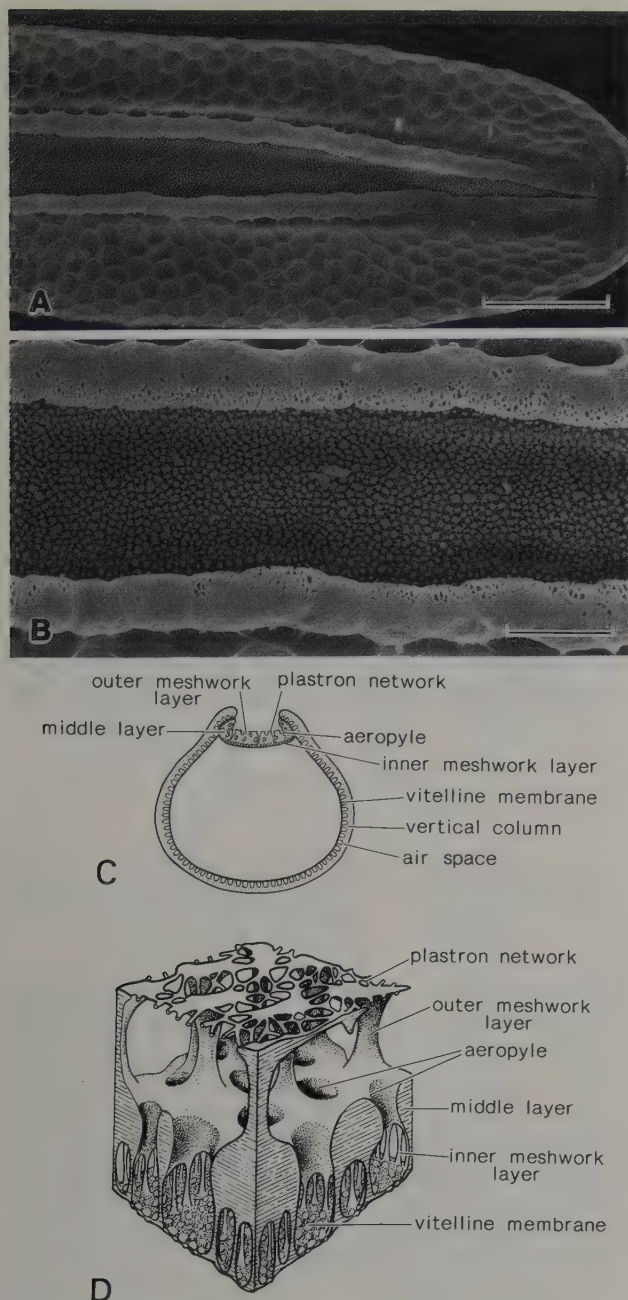


Fig. 2.52 Egg of *Chrysomya nigripes* (DIPT: Calliphoridae): A, part of egg showing plastron network between hatching lines (scale = 0.1 mm); B, detail of plastron network (scale = 30 μ m); C, diagrammatic cross-section of egg, showing continuity of air spaces through chorion beneath plastron network and all around egg within inner meshwork (after Chapman 1982); D, detail of structure of chorion between hatching lines (after Hinton 1963a). [A, B by R. L. Kitching; C, D by A. Hastings]

pressure against the chorion. The process is thus analogous to postembryonic moults, and in some insects special muscles are present to assist the process; these degenerate after hatching.

In a number of insects hatching is aided by cuticular structures, usually on the head, known as egg-bursters. Sometimes, as in Odonata, Orthoptera and Heteroptera,

these are present on an embryonic cuticle which is shed at hatching; in other groups they are present on the cuticle of the first instar larva. Egg-bursters usually take the form of spines or cuticular teeth, but in Acrididae a thin membranous region on the neck, the cervical ampulla, is expanded by blood pressure and exerts pressure on the egg membranes. Larval Lepidoptera gnaw through the chorion.

Postembryonic Development

The process of moulting divides the postembryonic development of insects into a number of instars. During each larval instar active feeding occurs and nutrient reserves are accumulated primarily in the fat body, but also in some cases in the haemolymph; increase in thickness of the cuticle during this period also probably serves as a way of storing some materials. As a result, the insect increases in weight and some increase in size may occur due to the unfolding of flexible cuticle, such as the inter-segmental membranes of hemimetabolous insects and the soft cuticles of caterpillars. Sclerotised cuticle does not increase in size, but expansion of the new cuticle at the time of moulting produces a rapid increase in linear dimensions. The relative increase from instar to instar is not constant although Dyar's 'law' suggests that various sclerotised parts of the body increase by a ratio which is constant for the species, often about 1:1.4 at each moult. This may serve as a rough overall guide, but more detailed studies have shown that different parts of the body even of one insect may increase by different relative amounts at one moult and may vary in the increase from moult to moult.

The definition of an instar has been the subject of controversy. One view defines the instar as the period from ecdysis to ecdysis, the other from apolysis to apolysis (Fig. 2.53). The former view has the strength of being easily recognisable and so is of general practical use, but when an extended period occurs between apolysis and ecdysis this definition obscures the real situation. The presence of a fully developed adult within the pupal cuticle is an obvious example; while it may look like a pupa it is functionally an adult (Fig. 2.54). This situation is more adequately described by defining an instar as starting at apolysis. Both views have their value and one can only counsel common sense.

The stage between apolysis and ecdysis is called the *pharate* stage.

It is convenient to distinguish the larvae of Exopterygota as 'nymphs' and some authors restrict the use of 'larva' to the immature stage of endopterygote insects. This, however, obscures the fundamental physiological similarities in the development of the immature stages. In both types the changes occurring at each moult are controlled by the same two hormones. Moulting hormone regulates the moulting process in all cases, but the body form is determined by the presence of juvenile hormone in the haemolymph early in the instar. A high titre of juvenile hormone at this time leads to another larval instar at the next moult; in the absence of juvenile hormone adult features are produced. Extra larval instars are

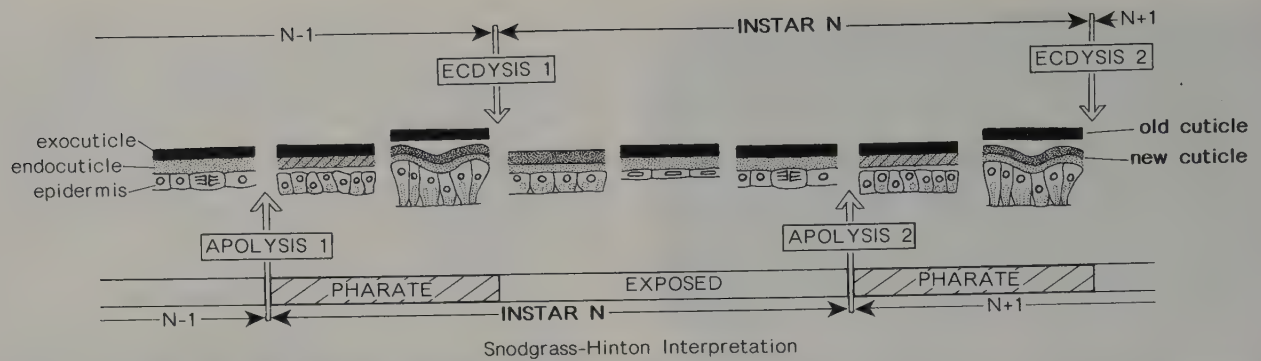


Fig. 2.53 Instar: diagram illustrating differences in definition of an instar according to the 'conventional' view and according to the Snodgrass-Hinton interpretation (after diagram by P. M. Jenkin).

induced, experimentally or naturally, if a high titre of juvenile hormone occurs in the last instar. The pupal stage of holometabolous insects results from a low titre of the hormone in the larval instar.

Metamorphosis

The term metamorphosis is most usefully applied to the change from larval to adult forms although it is sometimes extended to include all postembryonic changes in form.

Apterygota undergo numerous moults, usually more than 10, and continue to moult after they become sexually mature. There are no marked changes in body form between immature and mature insects and they are said to be *ametabolous* (without a metamorphosis).

Exopterygote insects commonly have four or five larval instars although gryllids and cockroaches have more. At each moult the wing pads and genitalia increase in relative size and although the larvae are generally similar in appearance to the adults the changes at the final moult are more marked. They are said to exhibit a partial metamorphosis or to be *hemimetabolous*.

In Endopterygota the larvae differ fundamentally in form from the adult. They increase in size at each moult, but do not exhibit any progressive change in form towards the adult. Four or five larval instars are common, and the last larval instar moults to the pupal stage before this, in turn, moults to adult. During the pupal stage there is extensive restructuring of the tissue. These insects are said to have a complete metamorphosis, or to be *holometabolous*.

In holometabolous insects many of the adult tissues develop in the larva from groups of epidermal cells called imaginal discs or buds. These cells do not produce larval cuticle and can be regarded as embryonic tissue which remains undifferentiated until it gives rise to adult tissue. This removes the constraints on body form which occur in hemimetabolous insects and permits the evolution of the larval stage independently of the adult.

The imaginal disc often becomes invaginated beneath the larval epidermis and development of the adult structure proceeds within the cavity which is formed and so is not visible externally (Fig. 2.55). Some structures form

relatively early in development, others not until the final larval instar. At the moult to pupa, the structures become evaginated and produce cuticle. The adult antennae, mouth parts and wings develop in this way.

In general, larval muscles are histolysed in the pupa, but the precise timing varies because some larval muscles have specific functions in pupal development. For example, most head and thoracic muscles in *Drosophila* larvae

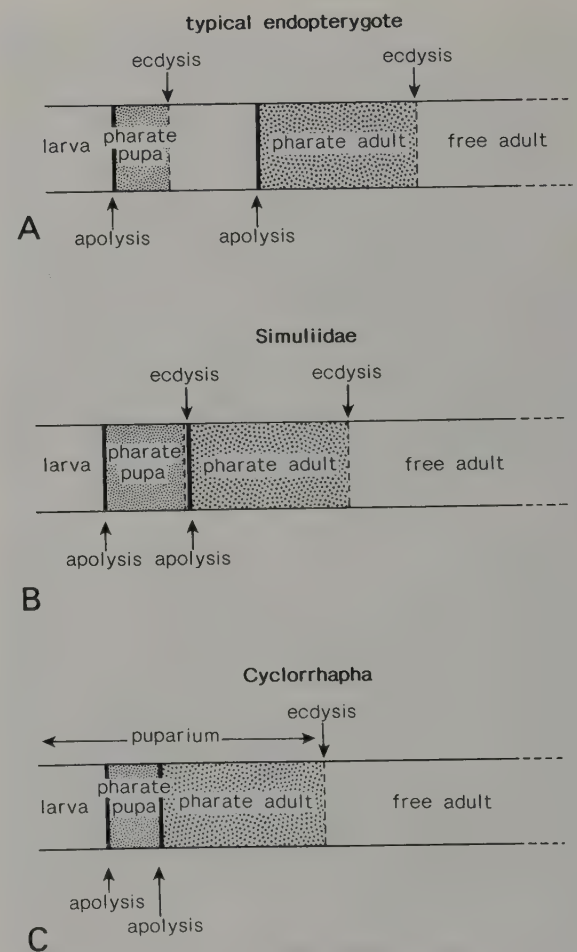


Fig. 2.54 Metamorphosis: diagrams showing differences in relative durations of pharate pupal and adult stages. [After Hinton 1971]

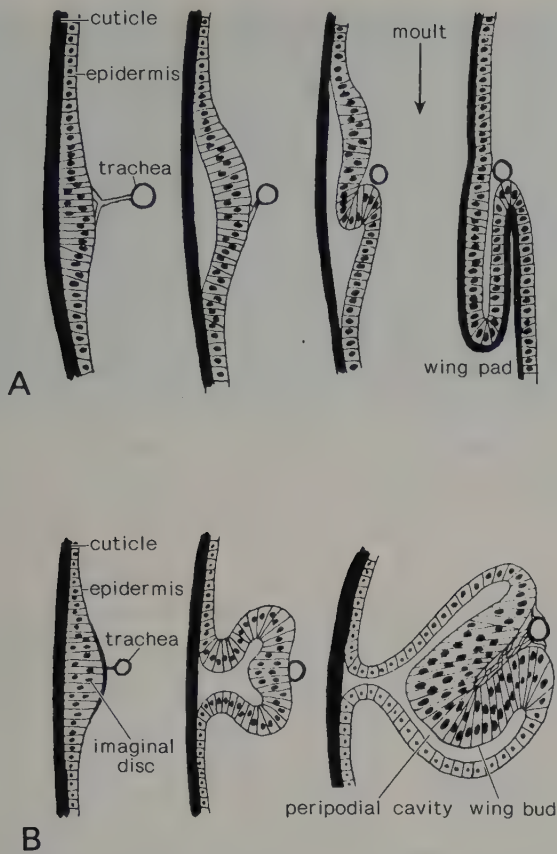


Fig. 2.55 Metamorphosis: development of wing in larval exopterygote (A) and larval endopterygote (B) insect. [After MacBride 1914]

break down before pupation, but the dilator muscles of the pharynx persist because they are important in evagination of the head at pupation; only after this has occurred do they degenerate. Adult muscles are often, perhaps always, present in the larva as rudimentary non-functional fibres. They become fully differentiated and functional in the pupal stage, although the flight muscles are often not fully developed and functional until some time after adult eclosion. This is why some insects have a teneral period during which their flight behaviour is not fully developed. The cuticle also undergoes changes during this period.

The alimentary canal is extensively remodelled at metamorphosis in species with different larval and adult

diets and the mid gut is probably completely renewed in all holometabolous insects by proliferation of the regenerative cells at the base of the epithelium. In most holometabolous insects the central nervous system becomes more concentrated at metamorphosis. This is accompanied by a forward movement of the more posterior ganglia and a shortening of the interganglionic connectives.

Pupa

In the pupa all the external features of the adult are recognisable even though they may not be fully developed. The appendages may be free from the body or held down by a secretion produced at the larva/pupa moult. These are known as the exarate and obtect conditions respectively. In addition, some pupae have articulated mandibles which, although they have no muscles directly attached to them, can be moved by the mandibular muscles of the pharate adult. This is the decticious condition; pupae without articulated mandibles are adecticious. Megaloptera, Neuroptera, Trichoptera and a few Lepidoptera have exarate, decticious pupae. All the other groups have adecticious pupae. The pupae of most Lepidoptera, Neuroptera, Nematocera and Brachycera are obtect while those of most Coleoptera, Hymenoptera, Siphonaptera and Cyclorrhapha are exarate.

Pupae with functional mandibles (decticious) are able to escape from the cocoon by biting through it. In some Lepidoptera the pupa forces its head through the cocoon using backwardly directed spines on the abdomen and a ridge or tubercle on the head. In many cases, however, the adult emerges from the pupa before escaping from a cocoon if one is present. Here, too, special mechanisms and structures may be employed in breaking out. Hymenoptera and Coleoptera use their mandibles to bite their way out and some weevils have an extension of the mandible to facilitate the process. The extension breaks off after emergence. Many fleas have a cuticular cocoon-cutter on the frons which is also deciduous in some. Some Lepidoptera produce chemical secretions to facilitate their escape from the cocoon.

In cyclorrhaphous Diptera the ptilinum facilitates escape from the puparium and also enables the insect to burrow to the surface of the debris in which it is often buried. The ptilinum is a membranous sac on the front of the head which can be everted by blood pressure while the rest of the cuticle of the head remains relatively soft. In the adult fly its position is indicated by the ptilinal suture.

General Biology

K. R. NORRIS

Migration by R. A. Farrow and V. A. Drake

In this chapter some account is given of the range of insect adaptations to various environments, the mechanisms by which these have been achieved, and the complex interactions between insects and other organisms, of both their own class and many other phyla.

ADAPTATIONS TO EXTREMES

Temperature Extremes

For poikilotherms, insects have shown a remarkable capacity to penetrate into the colder areas of the globe. Thus in the arctic regions many species live in areas that are frozen for most of the year. Life history stages in a condition of arrested development carry them through to the thaw, and growth and reproduction are crowded into the very few warm months. In some cases the completion of development has to be cumulative, and midges are known that spend seven years in the larval stage (Butler 1982). In spite of the long, rigorous cold period, adults of some species become very numerous in summer, and even north of the Arctic Circle in Canada and northern Europe, mosquitoes and black flies pose major regional problems (Gjullin *et al.* 1961). In the Southern Hemisphere such phenomena cannot occur, as there are no great land masses in the appropriate latitudes.

Collembola and mites have been found in moss, lichen and algae near the Shackleton Glacier (84°35'S) within 640 km of the South Pole (Wise 1964), but the most southerly record for a member of the Class Insecta is 68°35'S, where a flea, *Glaciopsyllus antarcticus*, has been collected from seabirds and their nests (Smit and Dunnet

1962). Little cold adaptation would be needed by bird fleas and lice living in warm, waterproof plumage, or in nests during brooding, but it would be otherwise for life history stages tiding the fleas over in the abandoned nest or in litter or crevices between nesting seasons. On Antarctica and its adjoining islands, free-living members of the Insecta are represented by only a few littoral chironomid flies. The brachypterous *Belgica antarctica* occurs in Grahamland as far south as 68°17', breeding in soil near penguin rookeries (Usher and Edwards 1984).

Remarkable adaptations are shown by pinniped lice. The Weddell seal, *Leptonychotes weddellii*, which lives around the shores of Antarctica, is infested by the louse *Antarctophthirus ogmorhini* (Fig. 3.1), which clings to the hairs on the tail, ankles, hips and hind flippers. The seals feed for lengthy periods in the sea, the lice then being constantly in contact with water at -2.0°C. In their cold-enforced inactivity, oxygen absorption from the water is sufficient for their respiration, but to survive they must also get blood feeds, and this they do when the hind flippers and nearby areas warm up during dissipation of heat generated by the diving activity by the host. The lice cannot breed while the hosts are at sea, but multiply rapidly when the seals haul out, especially in spring when the females pup and in summer when most of the population comes ashore. Then, despite brief feeding excursions by the seals, the female lice can mature eggs and the nymphs can grow. Although the haul out periods are relatively warm episodes in the life cycle of the lice they would still have difficulty in breeding were not their eggs capable of hatching at 0-4°C and other life processes able to proceed at 5-15°C.

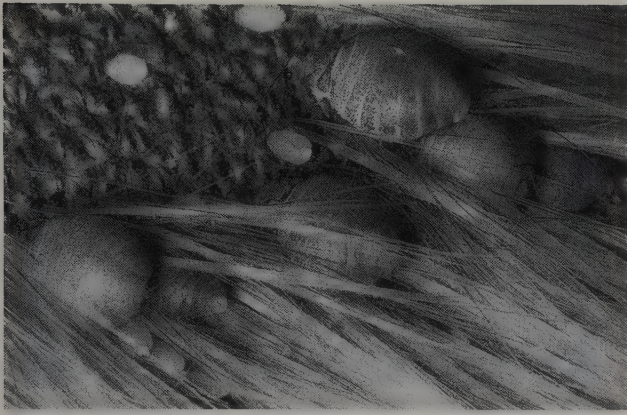


Fig. 3.1 *Antarctophthirus ogmorhini* (PTH: Echinophthiriidae) and eggs on Weddell seal, exposed by plucking hair; largest adults 3 mm long.

[I. Roper]

A somewhat similar life history is exhibited by *Lepidophthirus macrorhini* which infests the hind flippers of the southern elephant seal *Mirounga leonina*. This louse has a slight advantage in that the host lives in water several degrees warmer than that inhabited by the Weddell seal, and hauls out on the somewhat milder subantarctic islands to breed and moult, but to offset this, the elephant seal spends unbroken periods of 4–5 months at sea. During such cruises any eggs are destroyed, but some lice survive in burrows in the stratum corneum of the skin. They respire from the oxygen dissolved in the sea water and obtain blood feeds when body heat, generated during hunting, is being dissipated from the flippers (Murray and Nicholls 1965; Murray *et al.* 1965).

The subantarctic islands have a modest fauna of Coleoptera, Diptera, Lepidoptera and a few other groups, which are adapted to survive long periods of low temperature. Like *Belgica antarctica*, many of the species are brachypterous (Fig. 3.2) or apterous (Gressitt 1961), the strong winds and storms selecting against actively flying insects by carrying them into the sea or into unsuitable environments. Probably for similar reasons, flightlessness is common in small insects in mountainous areas of eastern Australia, and in the storm-swept regions of Wilson's Promontory.

Conditions over most of the Australian continent do not call for exceptional cold tolerance, though the southern winter precludes the occurrence of active stages of many species. The extremes occur in elevated areas of the south-east. Snow cover inhibits practically all insect activity, though adults of the wingless *Apteropanorpa tasmanica* (MECO: Apteropanorpidae) are commonly found moving about on snowfields in Tas. In snowfield areas many groups must overwinter as larvae or pupae in the soil, in logs, tussocks and other vegetation, and most grasshoppers probably do so as eggs in the soil. Whether the life cycle is annual, however, or spread over several seasons, all development is crowded into the warmer months. Then it is seen that the fauna is very rich in nectar-seeking Hymenoptera and Lepidoptera, stream-

haunting species with aquatic immature stages, cockroaches, grasshoppers, blood-sucking flies, and a wealth of Calliphoridae, breeding both in carrion and by preying upon the rich earthworm fauna.

In contrast, the mountains provide a haven in summer for one species when conditions in the lowlands become inhospitable. This is the bogong moth *Agrotis infusa* (LEPI: Noctuidae), which migrates in large numbers each spring from the western slopes and plains of N.S.W., Qld and Vic. to the high country of eastern N.S.W. and Vic. Westerly winds sometimes carry these migrants to the coast and out to sea where large numbers perish. But, in spite of occasional setbacks, moths progressively concentrate at granite outcrops on mountain summits and mass in deep crevices, which, it seems, have been used for millennia. They cluster on boulders in imbricate formation (Fig. 8.1), sometimes emerging at dusk to make short flights to drink but rarely feeding, so that fat body reserves become depleted. Moths disperse to the western slopes and plains in autumn, when, after rains, the winter annuals resume growing and provide suitable larval food. Energy reserves are restored by nectar feeding and oviposition occurs on suitable hosts.

Diapause

The bogong moths overwintering in the mountains are in a condition of reproductive *diapause*. Diapause is a condition of arrested development occurring in the annual cycle of many organisms, including a great number of insect species. Unlike quiescence, which is an immediate response to unfavourable conditions, such as drought or low temperatures, diapause is an anticipated interruption of development, programmed to occur in a particular ontogenetic stage by conditions experienced at an earlier

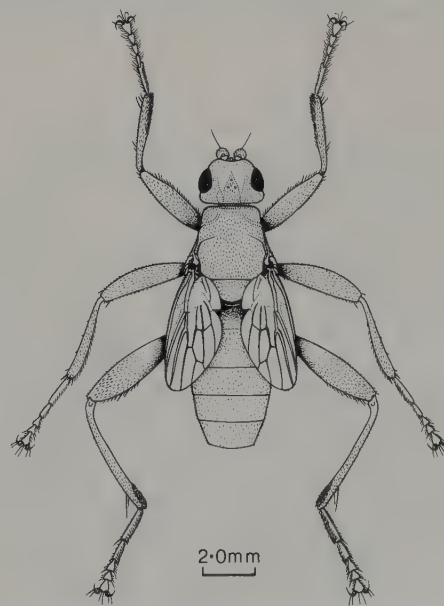


Fig. 3.2 Brachypterous fly, *Baeopterus robustus* (DIPT: Coelopidae), ♂ from Campbell I. (52°30'S).

[F. Nanninga]

phase of development. In quiescent insects, development is resumed as soon as conditions become favourable, but for those in diapause, exposure to particular environmental conditions, often different from those involved in the process of induction, is essential before normal development is resumed. Diapause is thus a more enduring phenomenon than quiescence and when invoked serves to maximise survival in areas with seasonal conditions unsuited to normal development.

In *univoltine* species (having a single generation each year) an obligate diapause may occur. The life cycle of the small plague grasshopper, *Austroicetes cruciata* (ORTH: Acrididae), affords an example of this type of diapause. This insect lives in parts of southern Australia with a cool, wet winter and a hot, dry summer (Fig. 3.3). The eggs are laid in the soil in the early summer and undergo partial development to a stage in which they virtually cease to lose water. They then enter diapause and remain in it even if unseasonable rains fall during the summer (absorption of water is essential to the development of acridid eggs). In the winter the low temperatures progressively break the diapause, but at the same time retard the development of the embryo until milder conditions prevail in the spring. Diapause and cold quiescence therefore ensure that the single generation of the grasshopper that can occur each year hatches from the eggs when conditions are most suitable for growth and reproduction of the active stages.

Contrasting with univoltine life cycles are those of *multivoltine* insects, which exhibit facultative diapause. For example the Australian plague locust, *Chortoicetes terminifera* (ORTH: Acrididae), normally passes through two or more generations per year. However, over most of its distribution area winter conditions are either too dry and/or too cold to permit the normal development of its active stages. Thus although eggs laid during spring and summer develop without interruption provided soil moisture is adequate, a variable proportion of those produced

during March–April have the capacity to enter diapause. Temperature and daylength experienced by the parent insects during their larval and early adult life determine the time of onset of diapause egg production, whereas temperature and moisture conditions prevailing in the soil during the early stages of embryogenesis determine the proportion of eggs that enter diapause. Although diapause is usually terminated before the onset of winter, prevailing low temperatures and/or dry conditions prevent hatching until the return of favourable conditions in spring. Eggs which fail to enter diapause may hatch before the advent of winter but, under the influence of decreasing daylength and temperature, the resultant nymphs enter a state of arrested development at the third nymphal instar. Development resumes in response to increasing temperature and daylength, so that the production of adults is delayed until spring. The possession of two separate but complementary overwintering mechanisms greatly enhances the ability of the species to survive in an environment that might otherwise be unsuited to permanent habitation.

The subtle interaction of diapause and quiescence with temperature and water availability in the Australian plague locust is shown in Fig. 3.4, exemplifying an extreme flexibility which maximises chances of populations of the insect persisting, one way or another, and which has been aptly described as 'bet hedging'.

In some other acridids, a third kind of diapause occurs in the adults. These overwinter in a state of reproductive diapause in which the gonads fail to develop until particular environmental conditions have been satisfied in the spring. Such a diapause prevents reproduction in the autumn when the offspring would fail to survive. (Andrewartha and Birch 1954; D. P. Clark 1972; Common 1954b; Wardhaugh 1972, 1980a, 1980b, 1980c, 1986]

Food Storage

Food storage is a survival mechanism that some colonial insects employ that cushions the impact of adverse periods in the environment. A number of kinds of ants (HYMN: Formicidae) in such genera as *Pheidole*, *Chelaner* and *Meranoplus* harvest seeds when they are temporarily plentiful, seemingly without much impact on the abundance of native plants, though sometimes a factor in afforestation and agriculture. The ants dress the nutritive portions of the seeds and feed them to the larvae, which metabolise the starch to fat and store it in reserves that are mobilised as needed into nutrient-rich oral secretions. Workers drawing upon these supplies in turn regurgitate them when solicited by other workers and reproductives. This process, known as trophallaxis (mutual feeding) is a vital factor in the biology of colonial insects. Although larval secretions may be important, the workers of most seed-harvesting ants can nourish themselves on other materials, but those of *Chelaner whitei* and *C. rothsteini* appear to sustain themselves entirely on food supplied by the larvae. Moreover larval food reserves are crucial to the overwintering of *C. rothsteini*. In areas such as western N.S.W. temperatures inhibit

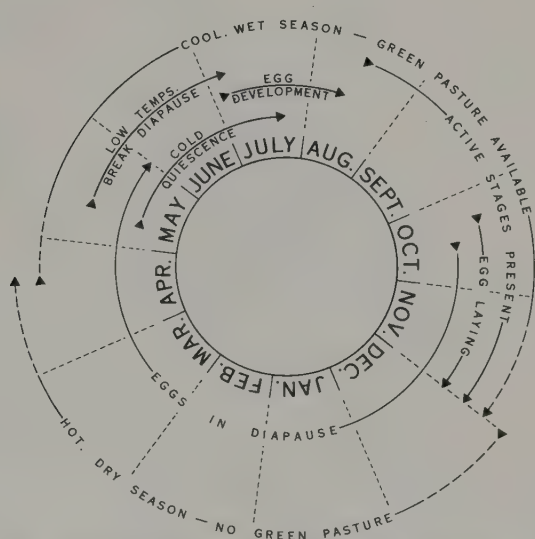


Fig. 3.3 The annual life cycle of the grasshopper *Austroicetes cruciata* (ORTH: Acrididae) in southern Australia.

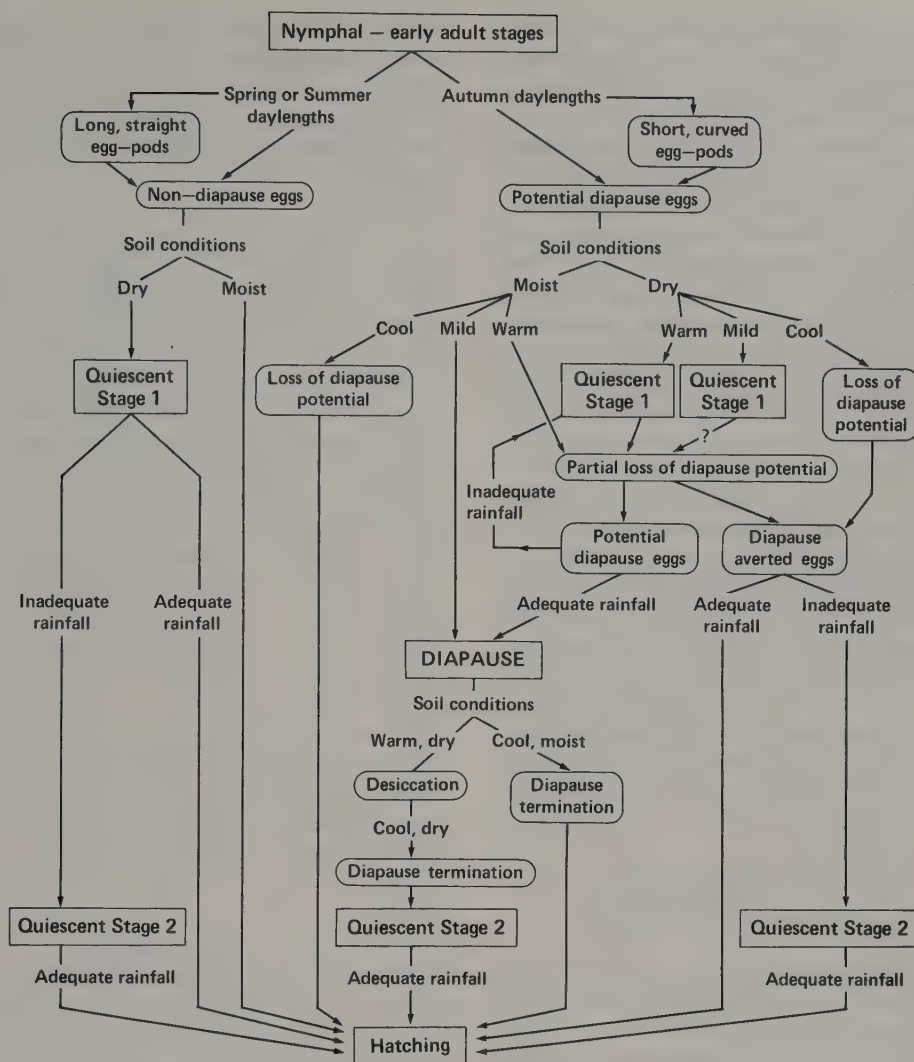


Fig. 3.4 Developmental pathways of the locust *Chortoicetes terminifera* in relation to environmental factors (after Wardhaugh 1986).

above-ground activity by *C. rothsteini* during the winter. Instead of meeting this situation by amassing large stores of seed, colonies of this ant feed all their harvest during the warm months to the larvae, so that winter is entered with little or no seed reserve but with a brood of fully fed larvae whose secretions carry the adult population over the winter (Briese 1982; Davison 1982).

Cave Life

An interesting extreme is found in the totally dark depths of caves (Hamilton-Smith 1967), where the permanent inhabitants, *troglobites* (= cave organisms) are frequently eyeless or almost so, but, in the Insecta, compensate by having long, slender antennae and legs and long bristles that accentuate their tactile sense (Fig. 3.5). Nearly one hundred species of arthropods are known from 47 caves in the Nullarbor Plain in southern Australia (A. M. Richards 1971a). Prominent among them is an eyeless

cockroach, *Trogloblattella nullarborensis* (BLAT: Blattellidae) (Fig. 3.6), which occurs from the 'twilight zone' into total darkness. Other troglobites occur in Tas., where there are species of eyeless or almost eyeless beetles (Goede 1967; Moore 1972). A considerable troglobite fauna, including bristletails, cockroaches, beetles and predacious and sap-sucking bugs also occurs in the extensive cave systems in the Mt Surprise area of North Qld (Howarth 1988). Insects restricted to the totally dark zones of caves are entirely dependent, directly or indirectly, on the fauna and flora of the outside world for their energy sources, which stem from bird and bat guano, decaying vegetation washed or blown into the caves, the carcasses of vertebrates and invertebrates that expire there, and the tissues and sap of deep-penetrating roots of epigaeic plants. The troglobites have become obligate inhabitants of the darkness. In this respect they differ from *troglophiles* ('cave lovers'), a term used to describe organisms that may occur in caves, even in darkness, but

which can also exist in other environments. Troglaphiles show no anatomical specialisation for a cave life. Notable examples are the Tasmanian fly *Arachnocampa tasmaniensis* (DIPT: Mycetophilidae) and some guanophile cockroaches in W.A. (Princis 1963). The term troglonexene has been applied to organisms that use caves as temporary shelters from unfavourable conditions. The term is not wholly appropriate in that it implies that such organisms are strangers to caves, whereas some may use them regularly. For example, two species of dragonflies, *Indolestes obiri* (ODON: Lestidae) and *Gynacantha nourlangie* (ODON: Aeshnidae) of the N.T., regularly spend their daylight hours in caves (Watson and Abbey 1980). So do some southern blowflies (DIPT: Calliphoridae), such as *Calliphora stygia* and *C. augur* when midday heat outside is inimical (Norris 1966). In Diptera this reaction is triggered by light intensity, rather than high temperatures. Just as photoperiod has come to entrain the onset of diapause, so the relatively noise-free diurnal rise and fall of light intensity has been exploited to trigger daily patterns of behaviour. In response to light intensity as a token, the tsetse *Glossina morsitans* (DIPT: Glossinidae) will forsake an illuminated chamber when the temperature climbs to a certain level, even if the darkened refuge is so much hotter than the illuminated one as to be lethal (Jack and Williams 1937). In nature, however, dark places are almost certain to afford some relief from high temperatures rather than to act as lethal traps.

ADAPTATIONS TO AQUATIC LIFE

Fresh Water

There is little doubt that the insects evolved as terrestrial animals, with a tracheal system appropriate to this mode of life. The widely-adopted aquatic life in insects is therefore secondary (Hinton 1976, 1977). In the Australian fauna all early stages are aquatic in the Ephemeroptera, Odonata (with one exception), Plecoptera, Megaloptera and Trichoptera, in many Hemiptera, Coleoptera and Diptera, and a few Neuroptera, Mecoptera, Lepidoptera and Hymenoptera. In addition there are some grasshoppers, such as *Bermiella acuta* (ORTH: Acrididae) (Fig. 24.14F), adapted for progressing on water surfaces, and, in other continents, aquatic or semiaquatic cockroaches.

Exclusively surface dwelling are the bugs of the superfamily Gerroidea (Chapter 30). These insects have coverings of hydrofuge hairs on the legs and body which enable them to rest and walk on the surface film, where many of the species spend their entire existence. Their methods of progression on the surface vary. Some walk much as other insects do on land surfaces. Others are basically skaters, steering with the rigidly trailing third legs, and propelled by the 'rowing' (synchronous) action of the middle legs. Fringes of bristles and retractable tarsal fans may assist propulsion. The gerroids are virtually the only full-time occupants of this niche (the *pleuston*, or guild of surface film dwellers), but a few other groups share the surface film at times, for example, the backswimmers or Notonectidae (HEMI) between dives, and the whirligig beetles of the family Gyrinidae, which

spend much of their time gyrating gregariously on the surface. The adults of a number of ephydrid and coelopid flies are quite at home on the water surface and their hydrofuge body surface ensures that they bob to the surface unaffected if swamped by a wave. The small flies of

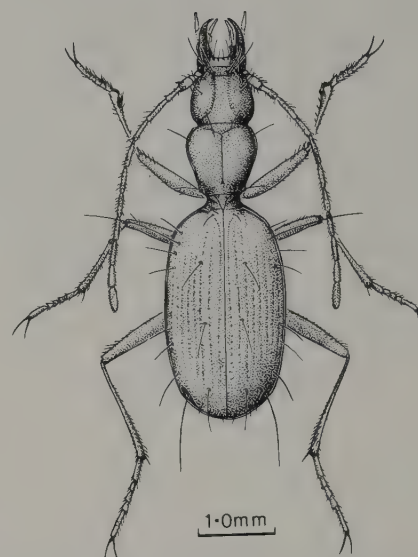


Fig. 3.5 A troglitic cave beetle, *Goedetrechus mendumae* (COLE: Carabidae). [S. Monteith]

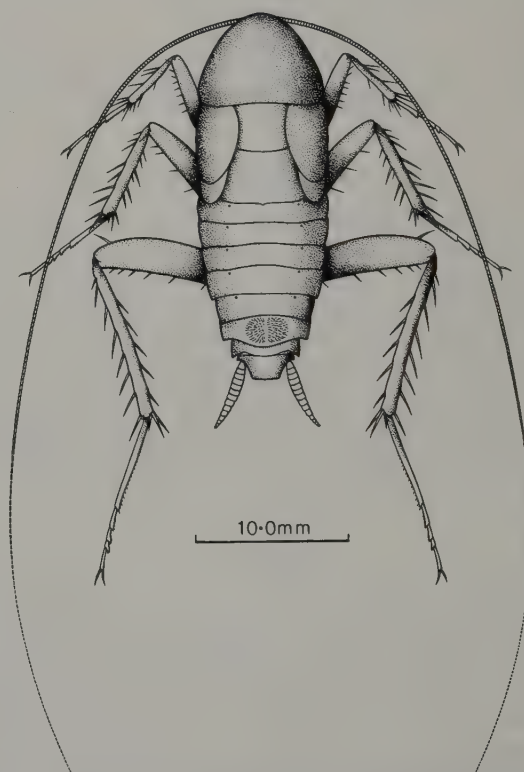


Fig. 3.6 A blind cavernicolous cockroach, *Trogloblattella nullarborensis* (Blattellidae), ♂. [F. Nanninga]

the genus *Hydrophorus* (DIPT: Dolichopodidae) often occur on the surface film. Mosquitoes and some other Nematocera are able to alight on water, and there are facultative pleuston members in other orders. Perhaps the most interesting are the riparian beetles of the genus *Stenus* (COLE: Staphylinidae), which have a unique jet mechanism to enable them to regain the bank should they fall on to the water surface (see p. 623).

Adults of aquatic insects have the legs converted in varying degree to paddles by the segments being fringed with hairs, and, in forms that dive, they are often flattened (Fig. 3.7). Most adult aquatic beetles progress under water by synchronous movement of the right and left legs of one or more pairs, but the adults of Hygrobiidae and Haliplidae retain the terrestrial habit of alternate movements of right and left legs. In diving insects the body is also often streamlined, and the antennae may be reduced in size and withdrawn into grooves, so minimising resistance while swimming under water. The elongate larvae of Zygoptera (ODON) and of mosquitoes swim by a fish-like wriggling. After breathing at the surface, mosquito pupae can make rapid descents by scooping with the abdomen after the manner of a crayfish. Larvae of some mayflies, such as *Mirawara*, have fans of hairs on the cerci and caudal style which they use as paddles by rapidly flicking the abdomen and straightening the tail, the reverse of the process in mosquito pupae. Most of the bottom-dwelling insects progress by crawling, but anisopteran dragonfly larvae can accelerate their progress by forcing jets of water from the rectum.

Most aquatic insects are *lentic*, that is, living in relatively still water such as swamps, lakes, ponds and slow-flowing streams, and relatively few are *lotic*, living in fast-running or turbulent waters. The lotic forms include the larvae of some Ephemeroptera, Odonata, Plecoptera, Megaloptera and Trichoptera, along with some adult Hemiptera and Coleoptera. Where turbulence is marked, lotic insects tend to live under stones, in crevices or in sheltered places on the bottom, but some that face the full force of the currents show special adaptations in the form of flattened bodies, strong clinging legs or, as in the Blephariceridae and Simuliidae (DIPT), special adhesive

organs, which give them security, if somewhat restricting their mobility.

Tracheal gills are a feature of many aquatic insect larvae. Most commonly they are developed on the abdomen, but they may be in other, even unexpected, places such as the rectum in some dragonfly larvae or on the mouthparts in certain mayfly nymphs. Tracheae in the gills or in the body of aquatic insects are necessarily pressure-resistant, and, to exclude water, the spiracles may be closed, haired, or too small to allow water to enter. Cutaneous respiration may be important, often involving a weakening or even total loss of the cuticular waterproofing mechanism—so vital to existence on land, but an encumbrance to an aquatic insect. Blood gills are present in some forms, such as chironomid larvae (DIPT), but are more important in water regulation and in maintaining ionic balance than in respiration.

Diving beetles and bugs entrap air periodically beneath the elytra and on the body when they visit the surface. The bubbles in such forms are in contact with the spiracles, and diffusion of oxygen into them from the water if they are smallish insects, supplements the original oxygen, so that the bubble may suffice for respiration for some hours or even days at low temperatures, but the nitrogen in the bubble is slowly but surely lost, without possibility of restoration by diffusion. Thus a return to the surface may be viewed not so much as for replenishment of oxygen as to renew the store of nitrogen and keep the surface area of the bubble above a critical limit. Elimination of carbon dioxide is not a problem, since this gas is highly soluble in water.

The larvae of mosquitoes of the genus *Mansonia* replenish their air supply by piercing aquatic plants with their respiratory siphons and drawing air from the aerenchyma and intercellular tissues. Larvae of the aquatic genus *Donacia* (COLE: Chrysomelidae) in northern Australia have a similar habit, puncturing the plants with their sharp urogomphi so that the posterior end of the body can be inserted into the air spaces.

Plastron respiration involves structures for holding a thin layer of air over surfaces of a life history stage that is passed in well-aerated water. It occurs in all elmid

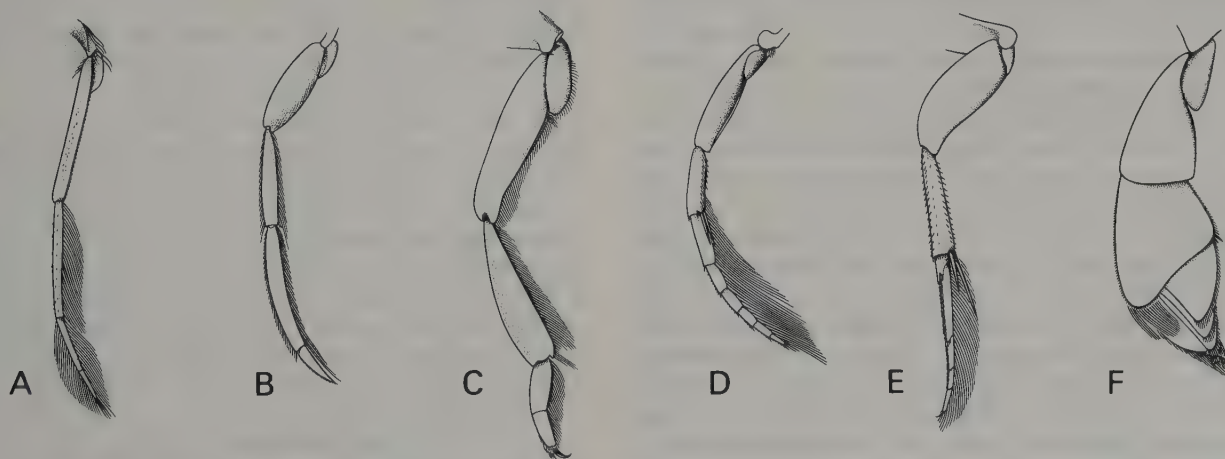


Fig. 3.7 Hind legs modified for movement on or in water. HEMI: A, Notonectidae; B, Corixidae; C, Belostomatidae. COLE: D, Dytiscidae; E, Hydrophilidae; F, Gyrinidae.

[F. Nanninga]

beetles, and is a feature of other beetles, some bugs and other forms. It is most perfectly developed in adult bugs of the genus *Aphelocheirus* (HEMI: Naucoridae), in which the ventral surface and large areas of the dorsum are covered with a very regular feltwork of submicroscopic hairs, each bent at a right angle. There are some 2.5 million of these per mm², and between and beneath them is permanently entrapped a very thin, almost incompressible layer of air, which is in contact with a complex spiracular system, finely haired to exclude water. Gas exchange by means of this plastron is so effective that in their well-oxygenated lotic environment, these highly active predators can remain permanently beneath the surface (Thorpe 1950). Such plastron-breathing insects are truly amphibious in that normal atmospheric respiration is resumed if they have to leave the water.

In dragonflies and some mayflies the last larval instar climbs on to objects near water, and the adult emerges there. In most other aquatic insects the pharate adult crawls out of the water on to rocks or plants to undergo the final moult. Some Ephemeroptera use the last larval skin as a raft during emergence, and chironomids and mosquitoes (DIPT) use the pupal exuviae in similar fashion (Fig. 3.8). The fully fed larva of the intertidal caddisfly *Philanisus plebeius* (TRIC: Chathamidae) attaches its case to the base of the coralline algae on which it had been feeding, and at the end of the pupal stage the pharate adult bites its way out and swims to the sea surface, where the adult emerges, capable of immediate flight (Cheng 1976). A remarkable specialisation is shown by the blackflies or Simuliidae (DIPT), in which the pharate pupa spins a hammock-like pouch on a surface under the water. When transformation is complete, the adult fly secretes gas beneath the pupal skin, and when this bursts and the bubble is set free, the insect rises to the surface in it, ready for flight.

Desiccation

A major problem to human and animal welfare in Central Qld is posed by the blackfly *Austrosimulium pestilens* (DIPT) which appears in swarms in the second week after summer floods in the intermittent rivers. The adult females lay while dipping the tip of the abdomen into the water during flight. Soil particles adhere to the egg as it sinks down into the mud. Although those that dry out die, eggs deeply buried in permanently damp patches of mud may remain viable for as long as 2.5 years. Floods invariably induce them to hatch, but the mechanism of diapause-breaking is not yet fully elucidated (Colbo and Moorhouse 1974).

Cryptobiosis is perhaps the ultimate in survival mechanisms in animals. This term is applied to a state of suspended animation, normal in the life cycles of small organisms such as tardigrades, rotifers and some nematodes, but also a feature of an African midge *Polypedilum vanderplanki* (DIPT: Chironomidae). In this condition the organism loses all its water and becomes inert, with no cellular activity at all. Larvae of the midge withstand at least brief exposure to temperatures of +102°C to -270°C, and they can survive immersion in pure ethanol for a day

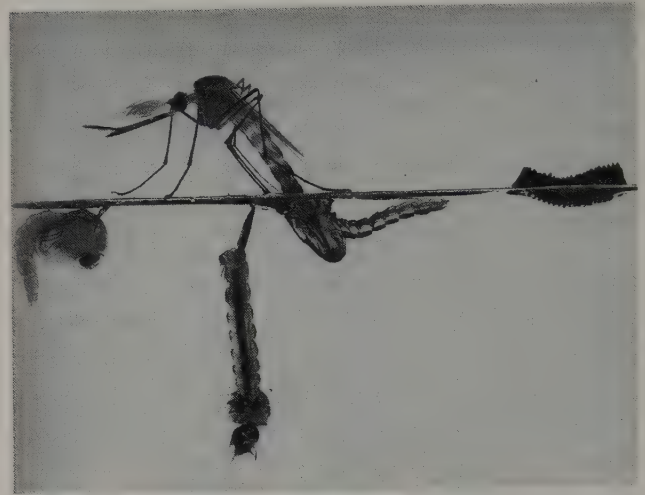


Fig. 3.8 Life history of the mosquito, *Culex fatigans*. From left to right: pupa, larva, adult emerging from pupal skin at surface, and egg raft; larva 6 mm long. [A. J. Nicholson]

or pure glycerol for a week. Larvae in a state of cryptobiosis will absorb water and become active when moistened after having been kept dry for three years (Hinton 1960). Cryptobiosis has not yet been detected in Australian insects, but there are some larvae that are notably resistant to desiccation. In Western Australia, at the end of summer, mature (fourth instar) larvae of the chironomid (DIPT) genera *Paraborniella* and *Allotrissocladius* burrow into the mud in hollows in granite outcrops and spin cocoons. They lose water rapidly for a few days as drying proceeds, but then the rate of loss falls markedly. Aestivating thus, they withstand mud temperatures as high as 57.5°C and survive many months without wetting (Edward 1986; Jones 1975). Adaptation to ephemeral waters is also seen in larvae of *Sclerocyphon bicolor* (COLE: Psephenidae), which inhabits intermittent streams in North Qld. Although larvae of most Psephenidae have the habit of clinging to rocks in fast-running water, and those of cool-temperate areas are sensitive to desiccation, larvae of *S. bicolor* are resistant to drying, and can survive flowless periods of up to six months if quiescent in cool, humid places under rocks in riverbeds. During four months in the laboratory third instar larvae have been known to remain viable after losing up to 78.4% of water (Smith and Pearson 1985).

Australia is second only to Antarctica in its aridity, and its vast and erratically watered areas must harbour many other insects with special adaptations for surviving high temperatures and prolonged desiccation. Thus it is of interest that one species of dragonfly occurs in a North Qld rainforest which is so continuously moist that the larval stages are passed in leaf litter on the ground surface, and that no other continent has produced such an adaptation in any other member of this order (see Chapter 17) (Watson 1982a).

Deep Water and the Sea

Despite the plasticity of the Insecta, only a few species of Chironomidae (DIPT) have succeeded in colonising the

depths of freshwater lakes. This is probably because all adult insects need free oxygen, and long ascents to the surface to permit adult emergence pose problems for final instar nymphs or pupae. The ascent of deep water Chironomidae is assisted by gas secreted inside the pupal skin, but such adaptations are few. No insects at all have colonised the ocean depths, perhaps because any other problems for smallish insects are capped by the ceaseless movement of the open sea.

A sparse fauna has colonised ocean beaches. Some of these are essentially terrestrial insects which breed in wrack or have become adapted to feeding on cadavers stranded near the high tide mark, or else have predatory larvae. The adults may invade wet sand, retreating when the waves return, like the coeloped flies, and eastern Australian tiger beetle *Cicindela ipsisilon* (COLE: Carabidae). Other beach insects survive temporary immersion by waves or high tides by displacing burrowers or digging for themselves. Others are well adapted to a life of periodical immersion. The really strong challenges lie in the rocky coasts and reefs, which are under constant assault by the sea (Cheng 1976). Since the turn of the century there has been speculation about the poor success of the Insecta in invading these zones and in colonising the sea. It now seems likely that turbulence and the ever-changing depth resulting from wave action and tides are major factors in limiting insect success in this zone. The problem is not confined to sea water, because the violent upper reaches of large rivers, such as the Amazon, are also comparatively poor in insect inhabitants (Hinton 1977).

Little credence is now given to suggestions that osmotic factors restrict insect invasion of the ocean, seeing that many species have become adapted to life in salt lakes and swamps where ionic concentrations are often very much higher than those of sea water. Nor does it seem that marine predators, once postulated as important in deterring insect invaders, could maintain an impassable barrier throughout 300 million years. In fact many delicate marine organisms survive in this frontier, and the soft-bodied and doubtless highly edible chironomid midges have been fairly successful in colonising reefs and rocky coasts.

It seems that success in fresh water is not necessarily a stepping stone to marine life. Thus no Ephemeroptera, Odonata, Plecoptera, Megaloptera or Raphidioptera and no species of the aquatic beetle family Elmidae has become marine. More than half the insects that have invaded beaches, rocky coasts and reefs are of terrestrial rather than fresh-water ancestry. They include Diptera of the families Tipulidae, Dolichopodidae and Canacidae and Coleoptera of the families Carabidae, Hydrophilidae, Melyridae, Salpingidae and Curculionidae. On the other hand the ancestors of marine Heteroptera (HEMI) of the families Saldidae and Omaniidae and the pelagic gerroid bugs, Coleoptera of the families Limnichidae, Hydraenidae and some of the Staphylinidae, Chironomidae (DIPT) and Trichoptera lived in fresh water. It is obvious why some habits and structural changes conferring success in fresh water have failed to provide an entrée to marine life. Thus colonists of the sea do not

include any of the divers that visit the surface to replenish air in compressible gills, or siphon breathers, piercing the surface film. Water levels in the intertidal zone vary too much and too frequently for such systems of air renewal to be employed. Insects drawing their air from plant tissues have also failed to invade the sea, perhaps because there would be a double problem: physiological adaptation and radical change in host plant group.

Except for such surface dwellers as bugs of the families Gerridae, Veliidae, Mesoveliidae and Hematobatidae (Gerroidea), the intertidal zone obviously poses problems of adjustment in insect respiration. In the sea there is an increased trend to the loss of water proofing mechanisms, so that cuticular respiration is even more common in marine than in fresh-water insect larvae. Plastron respiration also becomes increasingly common in pupae and adults. In the intertidal zone adult insects tend to rely partly on air trapped in the rock crevices in which they live. This is a feature of the tiny Qld omaniid bug, *Corallocoris marksae* (Fig. 30.53c), although it also respire from air entrapped beneath its wings. Another inhabitant of intertidal crevices is the limnichid beetle *Hyphalus insularis*, also diminutive, and living in interstices of consolidated coral sands of Qld coastal waters. At high tide these beetles respire from a store of air held in a compressible gill under the elytra, and also from air entrapped in a plastron composed of myriads of close-set, minute hairs spread over the body surface.

In the intertidal zone submergence akinesis is common. As the term implies, the insects become immobile when submerged. This reduces their oxygen consumption until low tide exposes them and enables them to resume normal respiration.

The high incidence of brachyptery and aptery in marine insects indicates that the power of flight, such a potent factor in the success of insects on land, is disadvantageous in the sea. Many intertidal bugs and Coleoptera are flightless, and so is a high proportion of the marine chironomid midges (DIPT). In some of the midges inhabiting sea coasts, flightlessness is compensated for by enhanced walking ability—not normally a strong feature of the family. Some chironomids that have retained the power of flight have it so modified that the males can only rise a limited distance above the water. The males of *Clunio marinus*, for example, seem unable to achieve an altitude exceeding 30 cm in dodging foaming wavelets and seeking their flightless mates. In this respect the most specialised forms occur in the genus *Pontomyia*. The pupae of these midges swim to the surface, where the adults emerge. The female is vermiform and structurally degenerate, but the mobile male (Fig. 3.9) has a unique type of locomotion. It skates on the surface film, supported on the tips of the stout, incurved middle legs and those of the stilt-like, backwardly-directed hind legs. The wings are modified into paddles which merely flick the relatively inert layer of air at the air–water interface. The fore legs are modified into ‘outriggers’, also barely skimming the surface, but keeping the stance of the male just at the right position to ensure the efficient operation of the wings. The powers of ‘flight’ conferred by these exquisite

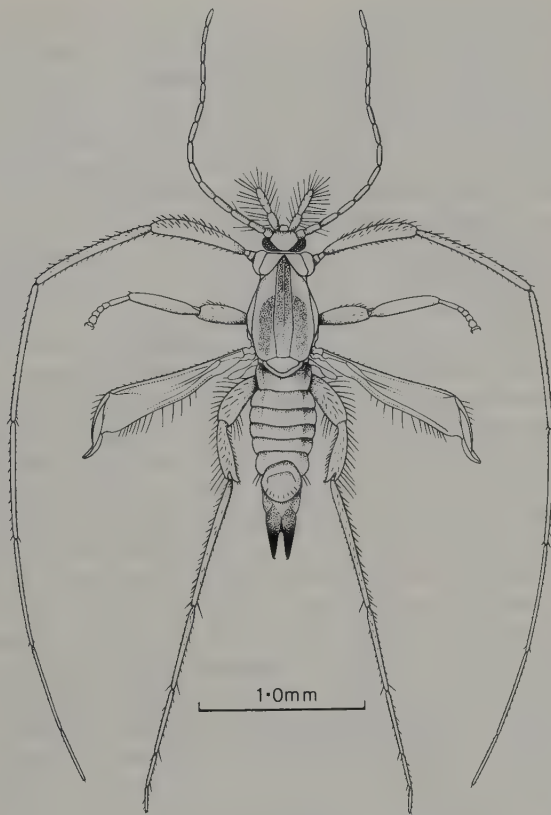


Fig. 3.9 Male of the midge, *Pontomyia* (DIPT: Chironomidae), which skates on the sea, propelled by its modified wings. [F. Nanninga]

modifications are sufficient to enable the male to reach the floating female, pick her up with his middle legs, assisted by the bases of the hind legs, and achieve a brief mating 'flight'. He then drops her not far from the rendezvous, and so her eggs are laid where resources are available for breeding.

Flying marine insects would be constantly in danger of transportation into areas where niches suitable for breeding are not available. Such an explanation of their commonly-lost powers of flight seems quite adequate for dwellers in rock crevices and reefs, but certainly not for the marine gerroid bugs, which have successfully invaded the sea surface by at least eight evolutionary pathways, and are all flightless. A high percentage of these were probably derived from forms that were already wingless, or from groups that commonly exhibit alary dimorphism. Significantly, most of the marine gerroids live in the relatively sheltered waters of inlets and inshore seas, where several of the Australian species of *Halobates* occur (Fig. 3.10). The exceptions form a group of five ocean-going species of the same genus (Cheng 1985). One or more of these apterous scavengers is found in abundance on all tropical and warm-temperate seas, sometimes great distances from any sizeable land masses. They 'row', with the plumose middle legs operating in synchrony, the hind legs trailing rigidly for use in steering. These bugs are untroubled by problems of respiration or osmoregulation. They are unsinkable because their hydrofuge body cover-

ing of microscopic hairs entraps enough air to bring them rapidly back to the surface if swamped. Their ability to jump 10–12 cm from the surface may help them to avoid wavelets and to reduce predation by fish. Powers of flight would obviously serve them better in such emergencies, but, from their universal aptery there seems little doubt that wings would otherwise be a disadvantage to their mode of life. Perhaps their diversion of resources into the huge legs required for skating precludes investment in effective wings.

Some marine Chironomidae (DIPT) have evolved physiological time clocks that fit their life cycle to an environment dominated by tides. In the North Sea, for example, the time of pupation of *Clunio marinus* is so geared to the regular monthly variations in moonlight intensity, that adult emergence occurs about every 15 days, when tides are low (Neumann 1976). Within the low tide period, entrainment with the day/night cycle limits the emergence of adults to periods when conditions are suitable for mating. Such cues would be irrelevant to insects that evolved in inland waters, because these habitats do not experience tides, but the evolution of marine chironomids exploiting the lunar cycle may well have started in tidal estuaries.

INSECT RELATIONSHIPS WITH PLANTS

Plants as Insect Food and Habitations

There is evidence that land plants may have appeared as early as the Upper Ordovician, and they were certainly well established by the mid Devonian. Remains of terrestrial arthropods—millipede-like forms—first appear in late Silurian rocks, Collembola, resembling certain modern forms, in the Lower Devonian, and possible Archaeognatha, along with myriapods, spiders, mites and other arachnids in the early Upper Devonian, some 378 million years ago. Thus the ancestors of the Insecta probably evolved in a terrestrial environment in which they

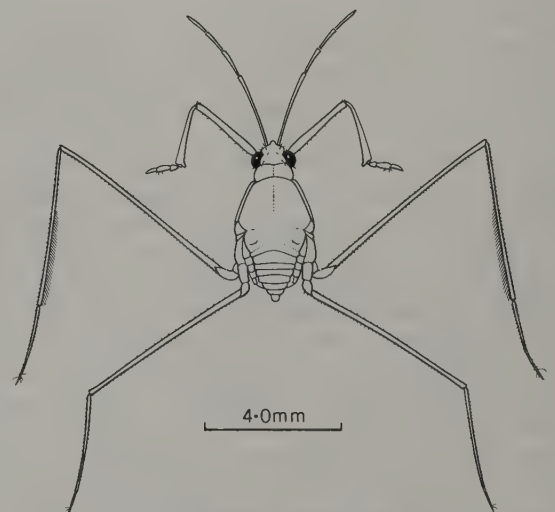


Fig. 3.10 *Halobates mjobergi*, an inshore marine gerroid (HEMI). [T. Nolan]

could become predators, feed on land plants and their remains, slime moulds, fungoids and algae in water seepages, or scavenge in shoreline debris (Anon. 1984; Gensel and Andrews 1987; Greenslade and Whalley 1986; Shear *et al.* 1984).

The early land plants were chiefly ground-huggers or dwarfish shrubs of simple habit, and did not offer much diversity to insects living on them, but a new dimension was introduced by the development of tall, arborescent plants in the Upper Devonian. The large trees that evolved then in the Pteridophyta and Spermatophyta provided not only an ideal environment for the evolution of flight in insects, but enormously increased the amount and diversity of tissue available on each unit area of land for colonisation. However, the exploitation of this new domain was not without its problems. The Insecta includes 16 orders in which predatory species are dominant or important, a larger, overlapping group of orders whose members are commonly scavengers or feeders on microbes, fungi, etc. and only nine orders composed predominantly of exploiters of living plants as food (Table 3.1). Obviously there are problems in making a breakthrough to phytophagy, leading many groups to take to scavenging or predation as pathways to more readily assimilable food, but the huge numbers of species in the successful phytophagous orders indicate that, once this and other difficulties are overcome, evolutionary radiation may be dramatic.

Special problems that face phytophage and predator alike in becoming arboreal are desiccation and attachment. The cuticular waterproofing mechanism of insects gave the group a potent measure of protection in habitats on the ground and on low-growing plants, but insects that moved into the new environment provided by large trees were exposed to higher risks of desiccation, despite the thin film of humid air surrounding the tissues of their hosts. To some, drinking of more free water must have helped, but the problem was met in various other ways, including the development of behavioural traits to avoid extremes of solar radiation and drying by air currents, the insertion of vulnerable eggs into living plant tissue, the use of silk to construct refugia, perhaps accompanied by leaf-rolling or case-making, burrowing in buds and stems, leaf-mining and gall formation. Some forms turned to making tube-like refugia of bodily secretions. Sap-sucking, as developed in the Hemiptera, also effectively met problems of water balance, and from it stems the production of a foam bath as a refuge. Some of these methods of avoiding desiccation are not available to arboreal predators, but, for phytophages, boring, leaf-mining and gall formation, for example, solved also the second problem, that of attachment. Otherwise arboreal insects have become adapted in various ways to improving their purchase on plant surfaces. The cursorial limbs of ground-dwelling insects are of little use to tree dwellers, and various structures have developed to augment gripping

Table 3.1 Feeding habits of Insecta (excluding Phthiraptera, Siphonaptera, Strepsiptera, pollen-feeders and blood-feeders) (after Southwood 1973, modified chiefly in accordance with the classification proposed in this book).

Order	Carnivorous	Scavengers, microbial feeders	Fungi	Algae & lichens	Mosses & ferns	Spermatophyta
Archaeognatha	+	+	+	+		+
Thysanura		*				+
Ephemeroptera	+	*				
Odonata	*					
Plecoptera	*	*		*		
Blattodea		*				
Isoptera		*				+
Mantodea	*					
Grylloblattodea		*				
Dermaptera	*	*				*
Orthoptera	*	*		*	+	*
Phasmatodea						*
Embioptera	*	*				
Zoraptera			*			
Psocoptera		+	*	*		
Hemiptera	*		+	+	+	*
Thysanoptera	*	+	*			*
Megaloptera	*					
Raphidioptera	*					
Neuroptera	*					
Coleoptera	*	*	*	+	+	*
Mecoptera	*	*				
Diptera	*	*	*	+	+	*
Trichoptera	*	*		+		+
Lepidoptera	+	+	+	+	+	*
Hymenoptera	*	+	+		+	*
Totals						
Major (*)	16	13	5	3	-	9
Minor (+)	3	5	3	6	6	4

power. They include prominent claws combined with adhesive setae on tarsal pads (COLE: Chrysomelidae), clinging empodia (NEUR: Chrysopidae), protrusible tarsal bladders (adult thrips, THPT) and abdominal and anal prolegs in the larvae of sawflies (HYMN) and Lepidoptera. In the latter, the prolegs are furnished with numerous minute hooks, or crochets. Silk is commonly used to strengthen attachment. Bugs may depend partly on the insertion of the proboscis for security, and, to avoid removal from the host plant, the nymphs of some mirids may extrude part of the rectum as a sucker. Some forms, such as scale insects and Aleyrodidae (HEMI) secrete a broad-based attachment from which they are quite unlikely to be dislodged by ordinary environmental forces.

Apart from the difficulties presented by desiccation and maintaining a grip on plants, phytophagous insects have problems of nourishment. As Lawton and McNeill (1979) state: '... plant-feeding insects live in a ... sea of food that, at best is often nutritionally inadequate and, at worst, is simply poisonous'. Insects have a high protein content, materials for which, in phytophagous forms, must be secured from a host composed predominantly of carbohydrate. Thus higher protein content in plant tissue usually makes for higher rates of growth and reproduction and longer survival of phytophages. Two pathways, via high protein content of plant tissue, have been suggested for the initiation of phytophagy in the Insecta: pollen feeding, and the colonisation of dead and dying tissue made protein-rich by micro-organisms during decay. Establishment of insects on plants by either route could have led directly to consumption of healthy tissues. Pollen feeding is thought to have given the Thysanoptera, at least, the entrée to phytophagy. Digestive problems of other ancestral phytophages are thought to be reflected in the dependence of many forms of a gut flora to assist them in dealing with their food, and indeed many Coleoptera and Hemiptera have mycetocytes, or special cells housing micro-organisms which may even be grouped into organs known as mycetomes. The micro-organisms harboured there supply essential amino acids and proteins, and they synthesise vitamins and sterols.

Plant Defences and Insect Attack

Evolution of plants has been greatly affected by pressures of herbivore attack upon them. The inherent variation between plants, and even within-plant variation in suitability as food have been seen as defence mechanisms in themselves, as they pose major tracking problems for insect herbivores and significantly affect their population regulation. Low nutritional status may contribute also, by prolonging feeding times and so reducing insect abundance by exposing them to natural enemies for longer periods. However in most cases it would be difficult to say whether nutritional inadequacy has developed in plants as an evolutionary consequence of attack by phytophages. Individual plants may be resistant to insect attack, often for reasons not readily discernible. For example, some trees of jarrah (*Eucalyptus marginata*) are

resistant to the jarrah leafminer, *Perthida glyphopa* (LEPI: Adelidae), fewer eggs being laid upon them, and many of the larvae from these eggs dying in the early stages of development. There are many other examples of insect-resistant plants within species.

Many plants have elaborated mechanical barriers against insect attack. Obvious physical defences include simple toughness of the leaf surface, which alone may be a problem for newly hatched mandibulate forms. Pubescence is another common form of mechanical defence, and, significantly, its occurrence is negatively correlated with poor chemical defences. Also important are hooked hairs, evolved to assist plants in climbing, but serving a secondary function as a defensive barrier against insect attack. Cultivated beans, for example, may have hooked hairs that impale small insects such as thrips, especially when the leaves chafe together in the wind. Glandular trichomes, or 'sticky hairs', may be very effective in trapping insects or clogging their respiratory apertures. In some *Medicago* species, for example, the exudates of glandular trichomes may be toxic to small leafhoppers and weevil larvae, as well as impeding them. However, hairs, even glandular trichomes, may be used by some insects specially adapted to grip them. Wax coatings on leaves may form effective defences against insect attack. Glaucous juvenile leaves of *Eucalyptus bicostata*, for example, have a waxy layer that provides protection from the chrysomelid beetle, *Paropsis charybdis*, which nevertheless has the ability to devastate the wax-free adult foliage. The wax on the juvenile leaves clogs the claws of the beetles and prevents them from maintaining a hold on the surface. Lignin, silica and corky tissues may also impose barriers against insect attack. [Crawley 1983; Denno and McClure 1983b; P. B. Edwards 1982; T. Lewis 1973; Mazanec 1974; McKinney 1988; Southwood 1973, 1986; Strong *et al.* 1984; Whitham 1983]

Mechanical defences against browsing vertebrates may be quite ineffective against insects. Large, pointed spines are obvious examples of anti-vertebrate barriers that pose no threat to insects. Nor are the stinging hairs of nettles any proof against insect attack. A classical demonstration of this is provided by the stinging tree or gympie, *Dendrocnide moroides* (Urticaceae), which is a serious hazard for man and other mammals that may blunder against it in rainforest margins. Horses, for example, have been known to die from massive contacts (Everist 1974). Yet between the stinging hairs the leaves of these plants may be heavily attacked by phytophagous insects enjoying untrammelled lives, as far as predation by vertebrates is concerned.

Once an insect has overcome difficulties associated with the superficies of the plant it may be confronted not only by problems of nutrient imbalance but by the presence in the tissues of chemical defence substances. Some of these, such as resins, tannins and silica may contribute to the indigestibility of plant tissues, as mentioned earlier. Others, such as alkaloids and cyanogenic glucosides are directly poisonous, and others again, such as essential oils, may act as repellents or feeding deterrents. Plant defensive chemical substances are classed among allelo-

chemicals, non-food materials by which organisms of one species affect the growth, health, behaviour or population biology of organisms of other species. Plants have developed a wide variety of chemicals to protect themselves from herbivore attack, but there is a problem in that they are trying to frustrate or poison physiological systems which are essentially similar to their own. This is reflected in the fact that, for the protection of systems critical to their own functioning, the defensive substances are generally localised in glands, latex or resin systems or in vacuoles or stored as inactive precursors which become toxic only when the tissues are damaged and thus lost to the plant anyway. As with man-made insecticides, however, phytophagous insects have shown a remarkable facility for developing immunity to plant allelochemicals. Thus several prominent insect herbivores attacking *Eucalyptus* species, such as *Paropsis atomaria* (COLE: Chrysomelidae), have been shown to be more or less indifferent to the concentration of the pungent eucalyptus oils in the leaves they consume. Likewise the intensity of their attack does not bear the direct relationship that might have been assumed to concentrations of condensed tannins and other phenols in the leaves. Coevolution has dampened the impact of the defensive substances in this case, and the genus *Eucalyptus* (*s. lat.*) also affords another example of ways in which the effect of plant defensive substances may go awry. Some insects not only shrug off the defensive aspects of 'plant defensive' substances, but sequester them for their own defence. Thus larvae of the sawfly genus *Perga* (HYMN: Pergidae) store a concentrate of essential oils in a large oesophageal diverticulum, and regurgitate it when disturbed (Fig. 3.11). The effectiveness of this defence is shown by the fact that the larvae are immune to predation by birds, whereas egg masses and adult insects, which lack it, are heavily preyed upon.

Another example of insects sidestepping plant defensive substances is provided by the cucurbit beetles of the

genus *Aulacophora*. The leaves of Cucurbitaceae contain chemicals known as cucurbitacins, which protect the plant from most insects, but *Aulacophora* species have become adapted to the cucurbitacins and use them as attractants and feeding stimuli. In so doing they have escaped from competition with other kinds of insects deterred by the defensive substances, and they may also have adopted the cucurbitacins to protect themselves, since all their life history stages are notably free of natural enemies, and adults of many species of *Aulacophora* are brightly coloured in bold patterns, perhaps advertising distasteful or toxic qualities. [Carne 1962, 1966; Crawley 1963; Morrow and Fox 1980; Waterhouse and Norris 1980; Whittaker and Feeny 1971]

Discussion of the subject of phytochemical barriers against insect attack is complicated by the fact that the defences of many plants are oriented at least as much against mammalian browsers as against insects. The essential oils that occur throughout the genus *Eucalyptus* are strong-smelling and distasteful to humans, and may reasonably be assumed to be repugnant to other mammals as well. The plants are not fed upon to any extent by modern, ground-dwelling browsers, marsupial or otherwise, and, of the arboreal marsupials, only the koala and the greater glider can subsist on an exclusive diet of eucalyptus leaves, thanks to selective browsing by which they avoid cyanide precursors, to special modifications of the caecum and its flora, and to the possession of a liver capable of detoxifying oils and phenolic compounds. The chemical defences of the genus *Eucalyptus* therefore seem to be far more massive than required to meet the modern challenge, and perhaps it is necessary to look at extinct, large-bodied browsers such as *Procoptodon*, *Zygomaturus*, *Palorchestes* and a number of others, both terrestrial and arboreal (as distinct from grazers such as *Diprotodon* and *Nototherium*) as the source of selection pressure required to initiate their development. P. B. Edwards (1982) and Macauley and Fox (1980) suggest that we must look to the past to explain this paradox of high levels of allelochemicals in a genus under heavy attack by habituated insect phytophages. Perhaps the catastrophic depletion of the marsupial fauna in geologically recent times is significant.

The anatomy and physiology of insects gives them a number of advantages over vertebrates in dealing with plant defensive substances. In regard to the genus *Eucalyptus*, the chemical defences are so much weaker against insects than against mammals that there are many thousands of Australian insect species that attack plants of this genus, without any obvious hindrance by their secondary substances. By contrast, no insect yet introduced into Australia is known to feed on these plants, and few insects of other continents attack Australian eucalyptus plants cultivated there. Plants of this genus introduced into other countries present formidable barriers to unadapted phytophages, and 'may remain immune to attack by resident insects for long periods of time' (Strong *et al.* 1984). The only challenge to eucalypt growers in other countries is the accidental introduction of habituated eucalypt phytophages from Australia.

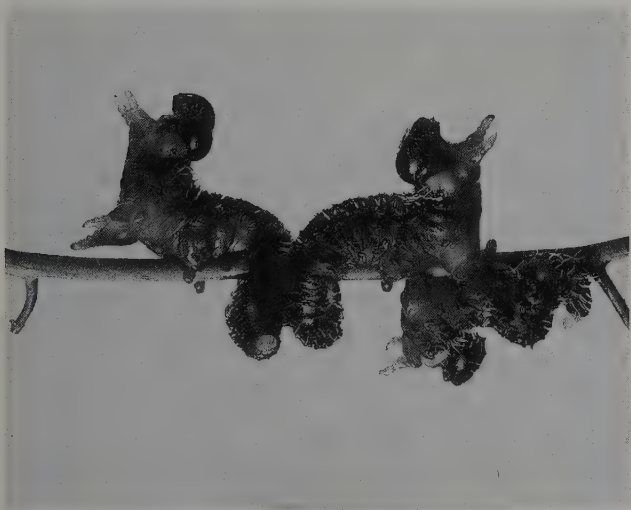


Fig. 3.11 *Perga* larvae (HYMN: Pergidae), 40 mm long, reacting to rapping on the branch; right-hand specimen has a large globule of regurgitated defensive fluid on the front of the head. [C. Lourandos]



Fig. 3.12 *Eucalyptus radiata* (foreground) defoliated by the phasmid *Didymuria violescens* (PHAS: Phasmatidae). [Z. Mazanec]

Disastrous results have followed such lapses in northern and southern Africa, Spain, Israel, New Zealand and California. Obviously the time scale is responsible for this situation. The Australian native insects have had millions of years in which to adapt themselves to eucalypt defensive substances, but the hundred years or so for which eucalypts have been exposed to insects of other continents has not been long enough to produce habituation.

Not only does indifference to the allelochemicals permit eucalypt insects to thrive in Australia, but, in the past, the presence of these substances in the plants must have given the insects a substantial measure of protection from destruction by mammalian browsers, which are frequently the unwitting destroyers of considerable numbers of foliage-infesting insects (Bernays 1982; Brown 1960; Hand 1986; Strahan 1983).

Injury to eucalyptus forests by native insects can be quite spectacular. Thus *Didymuria violescens* (PHAS: Phasmatidae) annually defoliates thousands of hectares of montane forests in south-eastern Australia (Fig. 3.12) and the jarrah leafminer *Perthida glyphopa* (LEPI: Adelidae) mines so extensively in the leaves of *Eucalyptus marginata* that each year vast areas of forest in W.A. appear as if scorched by fire (Fig. 3.13). There are many other insects that damage eucalypts extensively, including *Paropsis atomaria* (COLE: Chrysomelidae), *Anoplognathus* spp. (COLE: Scarabaeidae), and, in woodlands, *Perga* spp. (HYMN: Pergidae) and *Cardiaspina albitextura* (HEMI: Psyllidae). A number of studies have stressed the high average level of insect damage to eucalypts in Australia, and a number of significant decreases in growth increment have been demonstrated. Although examples of relatively low damage have been brought forward it is clear that insect attack is a major factor in eucalypt ecology. In fact it has been postulated that it is

responsible for preventing competitive exclusion, which is notably absent in eucalypt communities: herbivore damage is extensive enough to prevent any one species from becoming dominant. It has also been suggested that one reason for the severity of attack by eucalypt-adapted insects is that the leaves are generally very low in nitrogen, which is essential to the nutrition of the phytophages. This point, in relation to eucalypts, is stressed by Fox and Macauley (1974) and Morrow and Fox (1980) and, in relation to the survival of young insect phytophages in general, by T. C. R. White (1984). Accordingly the phytophages must have a considerable throughput of leaf tissue to ensure the completion of development. If so, then in many cases low nutritive status seems to be a dearly bought protection. Viewing the entire field of insect-eucalypt relationships it is difficult to take seriously a school of thought (Owen 1980; Owen and Wiegert 1976) that considers insect damage as increasing plant 'fitness', and propagates the opinion that plants 'encourage' infestation by phytophages for their own good (Brown 1960; Crawley 1983; Fox and Morrow 1983; Macauley and Fox 1980; Mazanec 1968, 1974; Morrow and LaMarche 1978; Ohmart *et al.* 1983a, b; Readshaw and Mazanec 1969; Springett 1978).



Fig. 3.13 Blotch mines of the jarrah leafminer, *Perthida glyphopa* (LEPI: Adelidae), in leaves of *Eucalyptus marginata*. The holes (mean length 4 mm) are sites from which larvae cut discs for pupal cases.

[M. M. H. Wallace]

Even more rich in species than *Eucalyptus* (*s. l.*) in Australia is *Acacia* (*s. l.*) (Mimosaceae). *Acacia* dispersed through Gondwana in the Mesozoic as shown by its strong representation in the Afro-Indian region and the Americas, as well as in Australia. *Eucalyptus*, which is almost precinctively Australian, may be no older than the Tertiary. *Acacia* could, therefore, bear relics of ancient defensive systems elaborated against long-extinct faunas of Australia and even of other continents: it is certainly more diverse and erratic in its confrontation with browsers than *Eucalyptus*. Several species that do not deter browsing by vertebrates are nevertheless toxic. The tissues of *A. georginae* contain the deadly monofluoroacetic acid and those of *A. glaucescens* contain cyanogens. Some other species are also toxic to vertebrates if consumed to excess, notably *A. salicina*, which has a high tannin content in the foliage. Plants of this genus are often notable for the high content of gums and tannins in their tissues, and perhaps massive levels of anti-digestive principles may rank high among their defences against insect phytophages.

As in *Eucalyptus*, *Acacia* species have many kinds of insects adapted to feeding on them in Australia, but, in contrast with the former, Australian *Acacia* species do not enjoy virtual immunity to insect attack when raised in other countries. This is due to the presence there of insect guilds already adapted to attack congeneric or closely related plants. In contrast, other countries lack close relations of *Eucalyptus*. Unlike *Eucalyptus*, a number of *Acacia* species in Australia have developed extra-floral nectaries, which may serve to retain ants as mercenaries for the general defence of the plant, though the evidence for this is not strong in Australia (Knox *et al.* 1986; New 1984b; Willis 1983).

There are many other plant genera in Australia with marked aromaticity and other qualities that probably indicate a long history of confrontation with vertebrates and insects. Some of the species of *Gastrolobium* and *Oxylobium* (Fabaceae) when actively growing generate in their tissues considerable quantities of monofluoroacetic acid, 27 g of leaves being enough to kill a 50 kg sheep. A number of marsupials, a native rodent and the seed-eating common bronzewing pigeon are resistant to this chemical, but the viscera of these vertebrates from 'poison' areas are highly toxic to domestic carnivores. The relationships of these plants to insects have not been investigated, but the seeds of all 42 species of *Gastrolobium*, including 27 known to be toxic, are adapted for ant dispersal as shown by their possession of elaiosomes (see later section). Thus it is likely that the Australian ant fauna contains an array of species resistant to monofluoroacetic acid. [Aplin 1967; Gardner and Bennetts 1956; King *et al.* 1978; Mead *et al.* 1979]

Bernays (1982), in an overview of plant allelochemicals in relation to insect phytophages, points out that the indifferent success of the Plant Kingdom in defending itself against insect attack is reflected in the many examples of plants being avoided by mammals but eaten by insects, in plant chemistry not significantly influencing species diversity of insects on host plants, in few plants having

notably low incidence of insect herbivores, and in the widespread adoption of defensive plant allelochemicals by phytophagous insects as feeding tokens or defensive substances.

Insect Phytophages and Disease Transmission

Disease transmission is another important consequence of insect attack on plants. Insects with chewing mouth-parts are rarely responsible for transmission of virus diseases, though they quite frequently transfer disease bacteria and spores of pathogenic fungi from unhealthy to healthy plants on their appendages and body. A notable exception is *Epilachna cucurbitae* (COLE: Coccinellidae) which, in Qld, is an efficient vector of squash mosaic, a virus disease of Cucurbitaceae. The virus transmitters par excellence are the Hemiptera, chiefly of the Sternorrhyncha and Auchenorrhyncha. In feeding, phytophagous Hemiptera inject saliva, which, even if devoid of infective micro-organisms, may result in serious effects on plant health through systemic action. However, virus transmission during saliva injection is by far the most serious consequence of feeding by Hemiptera. The mechanical damage to plant tissues may be negligible because the stylets often penetrate the tissues intercellularly in seeking direct access to the phloem, thus avoiding defensive substances elaborated in cells. If the insect, for example an aphid, is viruliferous, the plant is infected during feeding. If, however, a 'clean' aphid feeds on a diseased plant, it becomes infective in turn. In some species of Hemiptera, however, virus infection is acquired transovarially, the young being infected from the maternal tissues before birth or egg-laying. For example females of the Australian leafhopper *Austroagallia torrida* (HEMI: Cicadellidae) lay eggs yielding progeny able on hatching to transmit rugose leaf curl virus to a wide range of plants (Greber 1969; Grylls 1979).

Virus diseases of plants are also transmitted by some thrips. In this group the superficial plant cells are lacerated by the single (left) mandible, the coapted maxillary stylets reach in to attack deeper-lying cells, and liberated sap and cell fragments are periodically imbibed by the application of the mouthcone to the torn tissues. Sap is also imbibed through the tube formed by the maxillary stylets. Saliva injected into the mouth cavity may be connected with infection. Only the larval stages of thrips can acquire virus infection, but the adults arising from them are able to transmit it.

Galls

Australia is particularly rich in insects which form galls on plants: abnormal growth of the tissues, inside which some stages at least of the insect shelter and feed. Galls may occur in leaves, stems, buds or roots, and their shape and location are often characteristic of the plant and insect species involved. The gall is a response of the plant to chemical stimuli from the secretions of the insect. Gall insects occur principally in the Cecidomyiidae (DIPT) and Cynipidae and Chalcidoidea (HYMN), but among Australian Hemiptera there are some striking gall-formers in the genus *Apiomorpha* (HEMI: Eriococcidae) (Fig.

3.14) and a few gall-formers in the Psyllidae. Introduced Aphidoidea (HEMI) also include some gall-formers. Some Thysanoptera, Coleoptera and Lepidoptera also form galls. The agaonid wasps form galls in the flowers of figs, not visible by external examination. Any damage these insects inflict on their hosts is compensated for by their vital role in pollination.

Many galls on leaves, stem tips, leaf buds and flower buds of *Eucalyptus* are caused by the combined action of nematodes of the genus *Fergusobia*, and the larvae of acalyptrate flies of the genus *Fergusonina*. Fertilised female nematodes enter the body cavity of advanced female fly larvae, and give rise to larval progeny which invade the oviducts and pass out with the eggs when they are laid into eucalypt tissue. The nematodes then invade the tissues of the plants with the hatchling maggots and multiply asexually inside the developing gall. Male nematodes are produced in autumn and winter. They fertilise the females, which then complete the cycle by invading the body cavity of the fly larva. The relationship of the fly and nematode has been described as true *symbiosis*, both participants benefiting from it, the only loser being the *Eucalyptus* tree (Currie 1937). Galls are not necessarily harmful to plants, as witnessed by the fig wasps, although leaf galls may severely affect photosynthesis, and galling of flowers and fruits can affect seed output.

Coevolved Mutualism of Plants and Insects

The term 'coevolution' was proposed by Ehrlich and Raven (1968), who, in discussing aspects of community evolution, stated: '... what we would like to call coevolution is the ... interaction between two major groups of organisms, with a close and evident ecological relationship, such as plants and herbivores'. Implicit in the term, as coined, was the concept of mutual adaptation during the course of evolution. However, the interpretation of the word has varied somewhat according to the interests of authors, a common usage now current being to restrict its use to cases in which the evolutionary interactions have resulted in net benefits to both groups. It seems only sensible, however, to conserve the broad meaning intended by the propounders of the term, reserving for the special outcome of coevolution, involving mutual benefits, the expression 'coevolved mutualism'.

It has been claimed that the importance of coevolution in shaping insect-plant interactions has been overstressed, selective pressures not generally being strong enough to evoke mutual adaptations (Strong *et al.* 1984). A colourful image of the type of problem encountered in visualising adequate selective pressures is depicted by Janzen (1985): 'If the number of leaves you lose to a caterpillar is determined not so much by how your leaves taste as by whether there happened to be the right species of nectar-bearing flowers seven months ago in a different habitat, and next year it is determined by whether some other species of caterpillar suffered a disease epidemic to which your caterpillar is also susceptible, then evolutionary, to say nothing of coevolutionary, processes have a tough time maintaining the linkage they need to persist ... It is hard to coevolve a fine watch if God keeps pouring

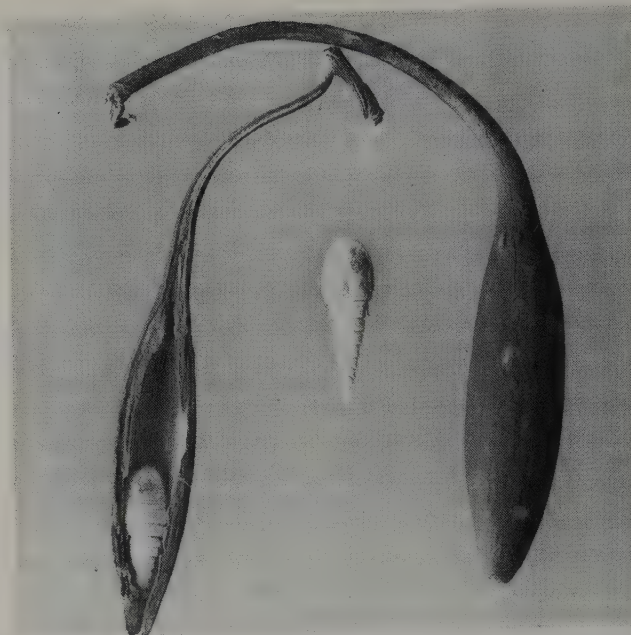


Fig. 3.14 *Apiomorpha pedunculata* (HEMI: Eriococcidae) ♀, from a eucalypt, and its gall; insect 25 mm long. [A. J. Nicholson]

sand into the works'. It seems unnecessary, however, to apply such generalisations to exclude the operation of coevolution from the examples dealt with in the present section because the mutualism developed by the plants involved is generally to groups of insects rather than to single species. That way the fluctuation of selective pressure resulting from the vicissitudes of individual insect species from season to season is minimised. [Gilbert and Raven 1975; Lincoln *et al.* 1982; Strong *et al.* 1984]

Myrmecochory. A striking example of coevolved mutualism is provided by the phenomenon of *myrmecochory* (literally, dispersal by ants). Myrmecochorous plants are those whose diaspores, or disseminules (bodies concerned with dispersal of the species) bear nutritive structures that induce ants to carry them back to their nests. Many have seeds with appendages known as elaiosomes (literally, oily bodies), which are not essential to the viability of the seed, but are attractive to ants as energy-rich food for their larvae (Fig. 3.15). The ants carry the seeds to their nests, divest them of their elaiosomes, and then either leave the seeds in the nest, or, more often discard them to the exterior, sometimes up to a metre or two from the entrance. Drupes, or diaspores with a fleshy covering around the seed, are also exploited by ants, though they appear to be better adapted to ornithochory (dispersal by birds) less probably to saurochory (dispersal by such omnivorous reptiles as *Trachydosaurus rugosus*). Some plants are described as diplochorous. Explosive dehiscence of the dried pod (ballistochory), gives the seeds a flying start, and the ants transport them to the nest from where they land.

More than 1500 species of Australian plants, representing 87 genera and 24 families are considered to be myrmecochorous. This adaptation is far more common in

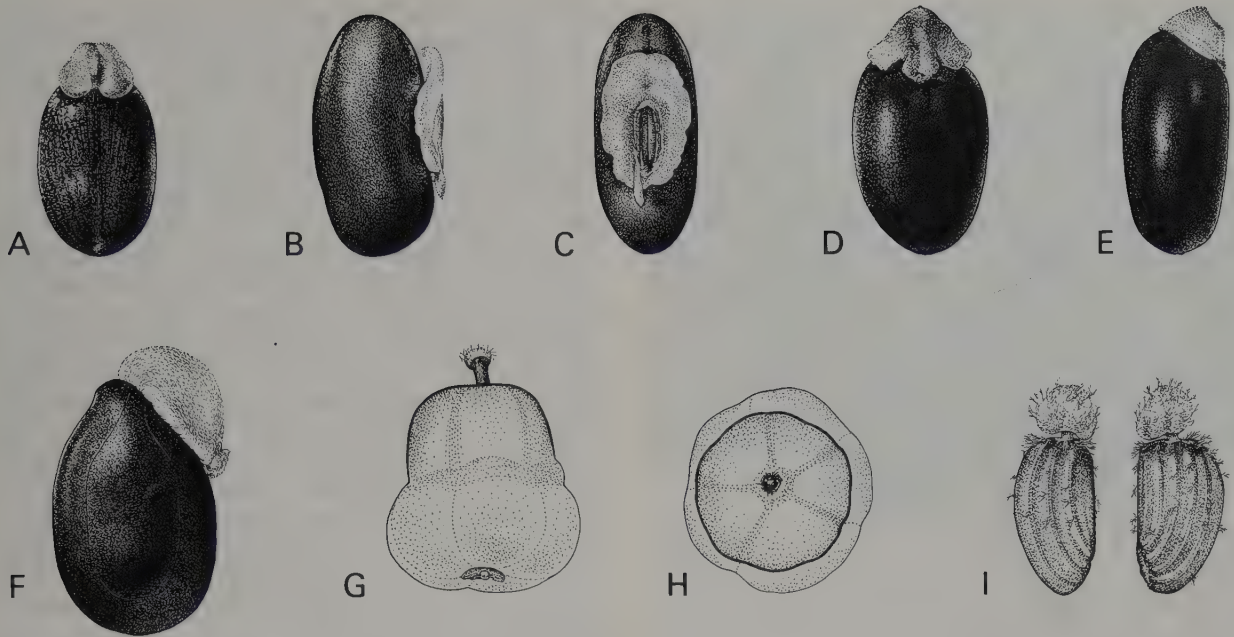


Fig. 3.15 Myrmecochorous diaspores: A–F, seeds showing ant-attracting appendages (elaiosomes); G, H, drupe, with distinct elaiosome; I, mericarps with terminal elaiosome. A, *Monotaxis linifolia*; B, C, *Kennedia rubicunda*; D, E, *Beyeria viscosa*; F, *Acacia linifolia*; G, H, *Leucopogon virgatus*; I, *Xanthosia pilosa*. [From R. Y. Berg 1975]

Australia than in other countries, and occurs especially in arid areas in lowland heaths, mallee understorey, dry sclerophyll forests and scrubby woodlands. It is quite distinct from seed harvesting, in that the seed proper is unharmed by the ants. Not surprisingly the seeds bearing elaiosomes are generally far too tough for the ants to make much impression on them with their mandibles, though the scarification they get during handling is sometimes sufficient to promote earlier germination.

Myrmecochory is considered to give the seeds favourable sites for establishment. The workers discard them after removal of the elaiosomes and often seek to hide them, it is thought, to prevent wasteful regathering by untrained foragers. To this end the experienced ants tuck the seeds away under fallen leaves, twigs, pebbles or in fissures, even moving them a second time to reduce the chances of their being rediscovered. In the process the seed usually lodges in a place where it has better chance of surviving after germination than if it were merely dropped on the soil surface. Small ants often provide seeds with an ideal germination site within their nests, because removal of the elaiosomes leaves them unable to grip the smooth, round seeds with their mandibles to carry them away for disposal.

The activities of myrmecochorous ants are favourable to the plant, in contrast with seed predation, in which only accidentally lost seeds and those gathered but surplus to requirements provide a chance of advantage.

The ants involved in myrmecochory in Australia are general foragers, distributed in many genera, and it seems that there are never any specific associations (Berg 1975, 1981; Milewski and Bond 1982; Westoby *et al.* 1982).

Ant-plants. In the Australian tropics occur interesting

ant-epiphytes which afford excellent illustrations of the outcome of coevolved mutualism. Perhaps the best known is *Myrmecodia beccarii*, which is found attached particularly to species of *Melaleuca* growing in mangrove and coastal swamps in the Cape York Peninsula. The tuberous main body of the plant is about the size of a large doubled fist. Its surface is tuberculous and bristly. Sparse tufts of lanceolate leaves grow from short stems on its upper surface. The surface of the 'tuber' is perforated by a number of small access holes, which lead into the chambered interior (Fig. 3.16). Some of the galleries inside are in the form of smooth-shelved structures, and others are tunnel-like, with warty walls. The plant's internal structure is not induced by ant activities, as it develops even when ants are excluded. However ants, usually *Iridomyrmex cordatus*, often occupy the interiors, and use the smooth-walled cavities for their brood chambers. Until recent years it was unclear whether the ant-epiphytes derived any advantage from the presence of guests in their *domatia* or residences: they seemed too robust to need defence. It is now clear, however, that their tenants provide nutrients in the form of debris from prey and dead nestmates which they stack in the cavities with tuberous walls. Radiotracer studies show that the tuberous structures absorb from the debris and ant excreta extracts which are translocated to the tissues in general. Thus the plants exact from their colonists a tribute in the form of nutrients and minerals, which their mode of growth precludes them from obtaining direct from the soil. The association of *M. beccarii* with ants enables the plant to invade niches where it is denied resources from plant debris that are so abundant in rainforest. In turn the relationship of the ants with *Myrmecodia* enables them to



Fig. 3.16 *Myrmecodia beccarii*, an ant-epiphyte of Cape York Peninsula.
[after Huxley 1982]

colonise open canopies where otherwise they would be disadvantaged by the scarcity of dead branches and accumulated litter for nesting sites. The symbiosis is only common where each participant would find it very difficult to thrive without the other.

Another very interesting ant-epiphyte is *Dischidia raflesiana* from Thursday I., which provides domatia for the ants. *Dischidia* leaves are sac-like and project horizontally from the stems. The ants use these hollow leaves to shelter their brood, and eventually for the disposal of debris which yields nutrients that are harvested by adventitious roots growing from the petioles into the cavities (Huxley 1982).

Another ant-plant association in Australia is that between *Camponotus quadricaps* and the tree *Endospermum formicarum* which grows in rainforest in the extreme north of Cape York Peninsula. Colonies are probably initiated by mated females invading branchlets following nocturnal nuptial flights. The ants chew holes in the terminal branchlets and excavate the soft central pith, ejecting it through the access holes. As the branchlet grows they excavate it progressively, but leave about 2 cm of intact tissue protecting the apical meristem. The newly excavated section is also provided with access holes, but only a few of these are kept in service at any one time, the oldest being allowed to become occluded by proliferation of plant tissue. The peltate (umbrella-like) leaves of *E. formicarum* bear a pair of extra-floral nectaries at their junction with the petiole, and the ants subsist entirely on a sugary fluid which exudes as clear droplets from these. They never hunt and never descend to the ground to forage, but in return for their shelter and sustenance they protect the plants, using their strong mandibles and acid spray to attack invasive insect herbivores and any vertebrates that menace their host (Monteith and Wood 1987).

To offset the presence of 'ant-plants' in the wet tropics

of Australia, there is a complete lack throughout the continent of mutually beneficial ant-*Acacia* associations which are such a prominent feature of African and Central American ecosystems. Typical of these is the mutualism between ants of the genus *Pseudomyrmex* and various Neotropical *Acacia* species. The ants bore into the inflated stipular spines (bull's-horn thorns) and excavate the soft central parenchyma, thus converting the thorns into secure domatia. Once established, the ants defend the host plant most vigorously, and the least disturbance brings the viciously stinging workers pouring out of the thorns to confront any intruder. The swollen-thorn acacias bear extra-floral nectaries which provide sustenance for the ants, and also special apical growths on leaflets, known as Beltian bodies (after T. Belt, a very early worker in this field), which contribute nutriment suitable for the ant larvae. So zealous are the ants in defending their host that they even prune creepers and other adjacent plants that might overgrow the *Acacia*, and in the process they also lower fire hazards. Although in Australia some species of *Crematogaster*, *Myrmecorhynchus* and other formicid genera live in hollow twigs, none can be said to be a significant defender of its host. Various other Australian ants harbour honeydew-yielding Hemiptera, and the green tree ant *Oecophylla smaragdina* vigorously defends trees of the various species it inhabits, but no structural modifications of the plants are ever involved in these interactions. It remains problematical, in particular, why this continent, rich in both ants and wattles should lack such striking associations as those seen in Africa and the New World.

Cross-pollination. Another very important field in which insects and plants exhibit coevolved mutualism is plant cross-pollination. This process, the fertilisation of one plant by the pollen of another member of the same species, produces higher fertility rates and more vigorous progeny than self-fertilisation. The rise of the flowering plants in the Cretaceous set the scene for some 130 million years of coevolution between large sections of the angiosperms and the Insecta, which alone among the arthropods had powers of flight to fit them for the role of cross-pollinators. Not all flowering plants turned to insect transportation of pollen (entomophily), the grasses (Poaceae) and many of the Cyperaceae, Plantaginaceae, Urticaceae, Juncaceae and the conifers adopting anemophily (wind distribution of pollen) for cross-pollination. Cross-pollination by anemophily is extremely wasteful, as vast quantities of pollen must be liberated to ensure that it takes place, unless the plant species involved is highly gregarious. Even casual and promiscuous flower-visiting insects are considered to be more efficient than anemophily in cross-pollination among sparsely dispersed flowers. In fact, beetles, which had been long established when the first flowering plants appeared, are thought to have been amongst the earliest pollinators (cantharophily), because they probably transferred pollen from flower to flower in the course of their predation on flower-haunting insects.

More specific relationships have arisen, principally amongst the orders Hymenoptera and Diptera which both

appeared long before the flowering plants, and the Lepidoptera, which did not appear until some 70 million years after them. Specialisation of the insects to enable them to exploit plant nectaries often involves the elaboration of the mouth-parts into extensible sucking mechanisms. The structure of the flowers often contributes to this tendency by forcing the insect to reach deep to secure the nectar, thus ensuring contact with the sources of pollen. Some flowers have intricate trigger mechanisms which are tripped by the insects as they strive to reach the nectaries, resulting in pollen or adhesive pollinia being dabbed on to their bodies. Pollen collection is, for the most part, incidental to flower visiting so far as the insects are concerned, but in a number of families of bees (HYMN: Apoidea) there are corbiculae, or pollen baskets—hair-fringed depressions on the tibia and basitarsus of the hind legs—or else a general hairiness of this area, when it is referred to as a scopa (pl. scopae). A scopa-like structure also occurs on the venter of leafcutting bees (HYMN: Megachilidae). Pollen so gathered is an important component of the food of larval apoids.

Entomophilous (literally, 'insect loving', but more specifically insect cross-pollinated) angiosperms have evolved inflorescences and mutualistic relations with pollinators that are of such diversity as to defy brief general description. Contrary to anthropocentric thinking, the coloured corollas, except in domesticated cultivars, are not adapted to appeal to the human eye, but rather to a usually restricted range of nectarivorous insects, whose visual powers may result in their seeing quite a different-looking object from that seen by man. Likewise the scents emitted by the flowers have a particular range of appeal, often fairly narrowly specific to potential cross-pollinators. Sometimes they simulate pheromones of a particular insect. In such cases the plant may be cheating in that benefits of the relationship are not mutual. Thus Australian orchids of the genus *Cryptostylis* emit a perfume so closely resembling the sex attractant of the female *Lissopimpla excelsa* (HYMN: Ichneumonidae) that the male wasps eagerly attempt to copulate with the flower. In the process they acquire a burden of adhesive pollinia (Fig. 3.17) which may be transferred to other blooms when they repeat the process of pseudocopulation. There is no evidence that the ichneumonid species benefits in any way, unless the male is excited by his experience to greater efforts in relation to his female conspecifics (Coleman 1928).

Not all insects are welcome visitors to entomophilous plants. Ants often appear to figure as a piratical group which has been confronted with defensive or distractive mechanisms by a number of flowering plants. There are various reasons why the roving worker ants are bad pollinators. They are flightless, highly territorial, and often quite local in their ecological impact, and they rarely visit another plant conspecific with the one whose nectar they tap. They also groom themselves thoroughly, thereby removing pollen grains, and, more importantly, in some groups they have cuticular secretions that contribute to nest hygiene by their antifungal and antibacterial effects but whose activity also inhibits pollen germination and



Fig. 3.17 Male of the wasp, *Lissopimpla excelsa* (HYMN: Ichneumonidae), bearing pollinia of the orchid *Cryptostylis erecta*, on which it is resting after having attempted copulation; male 11 mm long, excluding antennae. [A. J. Nicholson]

pollen tube growth. To reinforce these more subtle negative qualities, ants may also be aggressive bullies in the flowers, perhaps deterring some herbivores from damaging them, but offsetting this by treating herbivores and 'welcome' pollinators alike. In addition it has been shown that nectar robbing by ants may significantly reduce pollination in some plants. It is not surprising, therefore, that floral structure is sometimes bivalent in welcoming pollinators but discouraging ants from visiting the nectaries. Strategically placed slippery areas may debar ants from entering flowers, and allelochemicals in petal tissues may make them desist from chewing holes to bypass mechanical barriers. This may even be supplemented by the development of toxic or distasteful nectar to which flower-constant pollinators such as bees are less sensitive or can become adapted. Such defences may discourage not only ants but also many generalised flower visitors, particularly Lepidoptera, which otherwise dissipate the nectar, but in return are only poor cross-pollinators. A subtle supplement to such confrontation is the provision of extra-floral nectaries secreting palatable and harmless nectar which is eagerly sought by ants. The latter are then available to defend the foliage of the plant against herbivores, but are not in a position to interfere with the activities of effective pollinators.

Investment of resources into the development of extra-floral nectaries for the maintenance of ant bodyguards is worthwhile because herbivores are less likely to develop resistance to ant attack than they are to sidestep chemical and structural defences. This topic largely awaits study in Australia, but at Kalbarri in W.A. pollinators and ants visit different nectaries on the plant *Alyogyne hakeifolia* (Scott 1981). The extra-floral nectaries are only functional when reproductive structures are present that require defence, and although the garrison of biting ants does not entirely prevent damage to flowers it appears that it reduces it (Buckley 1982b; Proctor 1978; Rhoades and Bergdahl 1981).



Fig. 3.18 A sundew, *Drosera peltata*; unopened leaf buds at top; extended leaf right; adhesive hairs of leaf on left have closed over a trapped midge; height 26 mm. [J. P. Green]

Insectivorous Plants

Although almost all of the Plant Kingdom suffers attack by insect herbivores, several plant groups have succeeded independently in turning insects to useful account by evolving structures for capturing them and obtaining nutrients by digesting their bodies. It has been claimed that these adaptations developed in response to deficiency of certain nutrients in the ancestral environment—proteins, minerals and perhaps vitamins—but not all of the habitats involved are deficient in this way, and for those that are it could equally be argued that the adaptation of the plants has enabled them to move into nutrient-poor niches where they experience reduced competition.

Sticky Traps. The precinctively Australian genus *Byblis* has two species whose leaves, stems and sepals bear innumerable sticky globules on long hairs. These entrap insects and hold them until special digestive glands, found close to the surface of the stems and leaves, gradually digest their tissues. Predation by *Byblis* is described as passive, because only the adhesive structures contacted by the insect prey become engaged in dealing with it. Other sticky glands nearby do not become involved. Active traps occur in the sundews. Under this type fall some scores of Australian species of the genus *Drosera*. These inhabit bogs and peaty soils poor in nutrients, but also timbered country, rocky hillsides, and sometimes quite dry areas. On their leaves, particularly the upper sides, occur sticky glands borne on hairs, which entrap insects contacting them (Fig 3.18). Other nearby sticky-tipped hairs are then stimulated to bend over and participate in the digestion of the entrapped insect, hence

the description of predation by this type of plant as active. The bending of the hair is achieved by differential growth. The hair lengthens, but the surface remote from the prey lengthens more, in comparison with the nearer edge. Unlike *Byblis*, both the digestive and absorptive principles are invested in the glandular tips of the adhesive hairs, which extract all nutrients from the prey before returning to their pre-entrapment condition. Straightening of the hairs is brought about by further growth, the differential being the reverse of that by which they were initially bent over. *Byblis* and *Drosera* have devices that are known as tanglefoot, fly-paper or birdlime traps.

'Steel' Traps. A second type of trap is the 'steel' trap, seen in the plant *Aldrovanda vesiculosa*, a relative of *Drosera*, but aquatic, and not dependent on adhesives. The general principle of this trap resembles that of the celebrated Venus's-fly-trap of the Carolinas in U.S.A., *Dionaea muscipula*, except that it operates in water, and is much less robust. The plants occur in northern Australia and other countries. They are rootless, and float free beneath the water surface in the midst of reeds, rushes and other aquatic plants. There is a central stem up to 15 cm in length, around which leaves are arranged in whorls. Each leaf has a flattened petiole, broadening outwards to end in the half-folded, disc-like leaf proper, a bilobed trap which is protected from brusque attacks by four to eight stiff, bristle-like structures (Fig. 3.19). These heighten the resemblance of the plant to the hirsute, cylindrical inflorescence of a 'bottlebrush' of the genus *Callistemon*, to which it is so often likened. The inner surfaces of the terminal leaf blades have sensitive hairs, which, when tripped, cause the two lobes of the leaf to snap to and entrap small organisms. Progressive, slower closure squeezes out water and moves the victim inwards, and closer to surfaces secreting digestive enzymes.

Mouse Traps. Carnivory has also evolved in the bladderworts *Utricularia* and *Polypompholyx* whose snares are classed as of the mouse trap type. These plants occur in marshy areas or sodden soils with a high water table. Their submerged or below-ground parts bear numerous

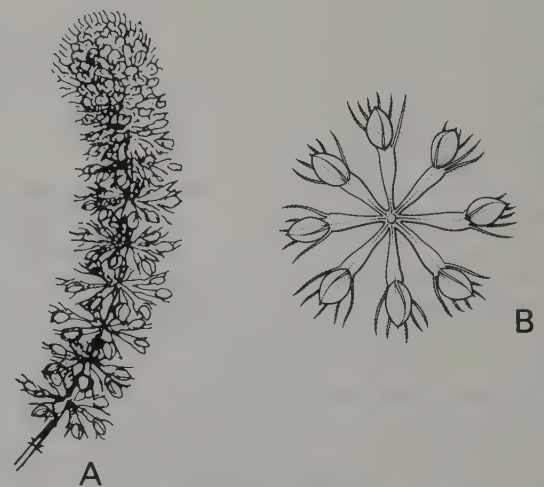


Fig. 3.19 *Aldrovanda vesiculosa*: A, entire plant, length about 15 mm; B, single whorl of leaves, with terminal traps. [after Slack 1983]

small bladders which are complex, but highly efficient traps for small aquatic organisms. Essentially, in *Utricularia*, the bladder has a terminal trap door or valve which fits snugly against a velum or transverse ridge of tissue to exclude water when the trap is set. Glandular structures in the wall of the bladder evacuate water from its interior, so that it partially collapses, placing the walls under stress. There are trigger hairs near the entry, and sometimes antenna-like structures thought to channel prey towards the entrance, where attractants may be secreted. When the tripping hairs are touched, the door opens violently inwards, the walls of the capsule spring outwards, and water is sucked in along with the prey. The door then swings back, and the trap is reset within 0.5 to 2 hours through the withdrawal of water. Secretions from digestive glands in the wall of the bladder result in the dissolution of the victim. In *Polypompholyx* the structures are essentially of the same nature, but there are 'wings' and a 'beak' over the trap door mechanism, and the prey is drawn in beneath these structures on either side of the bladder.

The bladders range in maximum diameter from 0.5 to 5.0 mm, and in many species are only big enough to catch protozoans, rotifers and copepods. The larger bladders of some species, however, can capture nematoceros larvae. If the prey is too big to be completely engulfed it is held fast and digested progressively, rather in the manner of some snakes dealing with elongated prey.

Pitfall Traps. Other kinds of plants have adopted a pitfall approach to insectivory, some of their parts having evolved into passive traps. A striking example, endemic to the south-west corner of W.A. is *Cephalotus follicularis* (Cephalotaceae). This small rosette plant grows in swampy country. It has two types of foliage, normal leaves between autumn and spring, and pitcher leaves (Fig. 3.20) which appear in spring and are fully developed when the normal leaves wither in summer. The phenology of the plant is thus well geared to exploit peak insect populations in a mediterranean climate. Pitchers growing in sunny places may be brightly tinted in red, green and white, which may give them a visual appeal to some insects, but really significant attraction is provided by nectar glands which occur in profusion on the lid of the pitcher and on the external and internal surface of the urn. The face of the pitcher below the lip has prominent vertical ridges, which, together with an edging of stiff hairs, are thought to guide insects up to the lip where ants and other crawling forms tumble over into the interior. They are drowned and digested in liquid in the bottom of the pitcher. Escape of the victims is made well-nigh impossible by sharp, down-curving claws projecting in from the rim, and by a polished collar-like, vertical structure rather like a valance, situated beneath the down-turned claws. This is rich in nectar glands which insects eagerly seek to plunder but it is so smooth that it is difficult for any of them to retain a footing.

What may be styled the classical pitcher plants of the genus *Nepenthes* (Nepenthaceae) occur in Madagascar and throughout the Malesian region. One species, *Nepenthes mirabilis*, occurs in Cape York Peninsula as an



Fig. 3.20 Pitcher leaf of *Cephalotus follicularis*, an insectivorous plant from south-western Australia. [V. Serventy]

undershrub in jungles. It has thick, broad leaves, whose stalks assist climbing by being winged and stem-clasping at the base. Tendrils at the tips of the leaves also assist attachment by looping around twigs or branches. From the down-turned ends of some of these, pitchers curve upwards. These are 5–15 cm long, and those nearest the ground have two vertical ridges, flanking the face below the lip, that may be fringed with hairs or bristle-like teeth. Like the ridges described in *Cephalotus*, the structures perhaps serve to channel crawling insects up to the lip of the urn. The lid of the pitcher may be brightly coloured, and have red tinges near the entrance which may serve to attract some insects. The rim of the entrance is corrugated with parallel ribs, which are brightly variegated in red, green and white, and doubtless add to any visual appeal of the entrance to insects. However, as in *Cephalotus*, the most potent attraction is provided by nectariferous glands, which occur on the under surface of the lid, and between the sharp, down-turned teeth arming the inside ends of the parallel ribs. The upper third of the interior of the urns is smooth and waxy, offering no foothold for insects. The walls of the lower two-thirds are rich in glands which secrete copious amounts of a fluid in which the abundant prey are drowned and digested. The lid excludes rain, which would dilute the fluid and disrupt the process of digestion and absorption into the wall of the urn.

Commensals of Insectivorous Plants. The impact

made by carnivorous plants on insect abundance in general must be very modest, but to offset even this they have a minor burden of insect opportunists, or commensals (sharing the food of another organism). These are either naturally suited to exploiting the nutrients afforded by trapped prey, or else have become specially modified to do so. In the former class fall muscoid Diptera, whose larvae are found thriving in the liquid in the pitchers of *Cephalotus*, and which may be able to escape on a moisture film to enable them to pupariate in the soil. In the pitchers of *Nepenthes* breeds a species of *Dasyhelea* (DIPT: Ceratopogonidae), *Sarcosolomonina papuensis* (DIPT: Sarcophagidae) and three species of *Tripteroides* (DIPT: Culicidae). The adult mosquitoes presumably fly unscathed into the pitchers, alight on the liquid surface, and after laying, make good their escape on the wing. Their progeny probably also fly out after emerging from the pupal skin at the liquid surface. The larvae of *S. papuensis* are probably deposited near the lip of the trap. When fully fed they presumably escape by travelling over the waxy upper part of the wall on a film of liquid, aided by the specialised spine bands or creeping welts, on the ventral surface.

The second type of insect opportunists exploiting carnivorous plants are Hemiptera, which have become behaviourally and structurally adapted to eluding capture by the sticky globules of tanglefoot traps. Australia has several bugs of the genus *Setocoris* (HEMI: Miridae) which are able to walk around with impunity amongst the adhesive hairs on the leaves of *Byblis* and *Drosera* species while they extract the juices from ensnared insects. Rarely these bugs become entrapped in the mucilage, but they can generally pull their limbs free and scrape themselves clean with the fore legs. It is suspected that some bugs of this group retain their ability to feed on the plant tissue. They also have a red-stippled colour pattern on a green ground colour, resembling the leaves of the host, and this doubtless reduces predation by birds. So they enjoy a high degree of security in an environment hostile to other insects. [G. Cassis pers. comm.; China 1953; Erickson 1968; Lloyd 1942; Marks 1980a; Slack 1983; Yeates *et al.* 1988]

INSECTS AS PREY AND PREDATORS

Many members of the Australian vertebrate fauna prey upon insects, and some provide notable examples of specialisation or of capacity for circumventing insect defence mechanisms.

The rifle fish (more commonly but less aptly known as the archer fish) of northern Australia (species of the genus *Toxotes* (OSTEICHTHYES: Toxotidae) exploit two life zones to achieve insectivory. Their ridged tongue is coapted with a groove in the roof of the mouth to make a squirting mechanism. At the surface the fish spurs water into the air to bring down roosting or flying insects (Fig. 3.21).

Among the mammals, the extant Dasyuridae are almost all insectivorous, size being no bar to success, since *Ningau timalei*, of the Pilbara spinifex country in north-

western Australia, is about one-third the size of a house mouse, but preys largely on centipedes and robust insects, subduing sclerotised, spur-bearing grasshoppers larger than itself by delivering repeated bites in vital areas. A notable exploitation of wood-boring insect larvae has been achieved by the striped possum, *Dactylopsila trivirgata* (Petauridae), which gouges away bark with its chisel-like incisors and extracts beetle and moth larvae from their tunnels, picking them out with its long tongue or the elongated fourth digit of the hand. The bats (Suborder Microchiroptera) generally hunt by echolocation, and one species, the mouse-eared bat *Myotis adversus* (Vespertilionidae) has perfected this technique to the point where it can prey on aquatic insects by scooping them up from smooth water surfaces with its large, clawed feet. The adaptive capacities of insects are, however, shown by the fact that some pyralid and noctuid moths, lacewings and crickets respond by evasive tactics to the ultrasonic pulses of hunting bats. A nice twist to insect-bat interrelationships is that some sphingid moths, known to be distasteful, advertise this to diurnal predators by warning coloration, but after dark, when visual cues are valueless, they emit ultrasonic clicks which disrupt the hunting activities of nearby bats, either by warning them of distastefulness or possibly by interfering with their integration of sound signals.

Mammals may adjust themselves to consuming insects that contain repulsive chemicals or potent defensive toxicants. Thus in Central Qld the brushtail possum, *Trichosurus vulpecula* (Phalangeridae), goes unharmed after consuming the larvae of the sawfly, *Lophyrotoma interrupta* (HYMN: Pergidae) which are not only redolent of the oils of the eucalypts they feed on, but also contain the curious cattle-killing octapeptide, lophyrotomin (Anon. 1988a; Common 1988; L. A. Miller 1984; Oelrichs *et al.* 1977; Popov and Shuvalov 1977; Roberts 1932; Strahan 1983).

Insect predation by birds is probably significantly greater than that of all other groups of vertebrates put together. Its zenith is reached by the swifts, which hawk for flying insects and are so specialised as to be incapable of any other form of predation. One species, the fork-tailed swift, *Apus pacificus*, nests in northern Asia, but in the non-breeding season, dependent on movement of air masses, it may appear in enormous flocks over the Australian continent. These birds never alight in Australia. They drink on the wing by scooping up water in their bills, and almost certainly sleep on the wing at high altitudes. Their energy-demanding mode of life requires that they consume vast quantities of flying insects, including migrating pests, but there is no way of measuring their impact.

The importance of the resident Australian bird fauna to insect abundance largely remains to be assessed because significant research has been carried out mainly in the cool-temperate forests of the Northern Hemisphere. Birds are usually highly seasonal in their breeding and unable to reproduce outside of this period to avail themselves of upsurges in insect abundance. They also tend to prey indiscriminately on host and natural enemy alike, which



Fig. 3.21 Juvenile of rifle fish, *Toxotes* sp., bringing down midge.

[A. Hastings]

greatly complicates the interpretation of their real importance. The general view in relation to pest control is that they can exert a controlling influence if insect numbers are relatively low, and so can extend intervals between outbreaks, but the effectiveness of their predation breaks down in areas where insects have become abundant. Despite the equivocal nature of the evidence for the impact of bird predation on insect pest status, many bird lovers cling to a defensive belief that it is invariably beneficial. This is far from true. For example, the pied currawong, *Strepera graculina* (Cracticidae) may prey seasonally on phasmatid pests when they become abundant in montane eucalypt forests in south-eastern Australia. These birds, which, anyway, are voracious poachers of the young of many species of smaller insectivorous birds, can keep phasmatid numbers low if they remain where the insects are scarce, but, instead, they tend to move to areas where the phasmatids are in plague proportions and the pickings are good, but where they can make no impact. Thus the phasmatids remaining in the forsaken areas are free to multiply to plague proportions. Even the insectivory of this bird therefore runs counter to forest welfare, yet in Frith (1976) it is ambiguously stated that '... it is thought, they prey significantly on two species of stick insects ...'.

Another example of maleficence of a bird due to its predation on insects is afforded by the yellow-tailed black

cockatoo, *Calyptorhynchus funereus* (Cacatuidae), which uses its powerful bill to excavate living trees in search of the very large and nutritious insect larvae such as those of the moth, *Xyleutes boisduvali* (LEPI: Cossidae). Its description by Leach (1929) as a 'valuable forest saving bird' was probably not even true in those days, but modern silvicultural developments have made it into a significant pest. Because of the amount of wood shorn away by the cockatoos when searching for the larvae, high percentages of eucalypt saplings in plantations are subsequently windthrown (S. H. Anderson 1979; McInnes and Carne 1978; Otvos 1979; Readshaw 1965, 1968).

Vertebrate predation on insects may have harmful consequences. For example some insects are intermediate hosts for helminth parasites, some ants and beetles also fill this role for several poultry tapeworms, and likewise certain cockroaches and beetles for roundworms of sheep, cattle and pigs. Similar relationships between insects and vertebrates must be widespread in the native fauna, but they have been little investigated.

Spiders (Araneae) are undoubtedly the most important invertebrate predators of insects, and since the Palaeozoic the two groups have evolved together. This has left strong marks on a number of spider groups in the form of snaring methods obviously aimed at insects, and in associated anatomical and behavioural characteristics, but it has made less obvious impact on the Insecta, unless one

views the development of caducous scales in the Lepidoptera as partly an aid to eluding capture in webs. Spiders may be hunters which pounce on prey encountered, or ambush or stalk it. Otherwise they make snares of extremely diverse design, ranging from trip threads radiating from burrows or refugia, which when touched alert the spider to emerge and seize the passer-by; through sticky spring-threads, which snap when an organism blunders against them, and hoist it upwards towards the spider's refuge; through lace-like shawls into which crawling organisms tumble, and flying or jumping insects project themselves; through knock-down labyrinths of dry silk which intercept flying insects and make them fall on to a horizontal platform patrolled by the spider, and finally to the orb web, with radii of dry silk on which the spider walks when harvesting flying insects entrapped in the sticky web spun in spiral or other patterns. Many of the devices are not obviously oriented towards the capture of insects alone, although this group is undoubtedly foremost amongst the prey. Only labyrinths and most orb-webs appear to have certainly evolved in response to the evolution of wings in Insecta. Orb-webs occur in the Araneidae and the Uloboridae. The former quickly subdue entangled prey with the fangs, but the latter have lost their poison glands and instead rapidly ensnare their victims in copious layers of silk. Some uloborid orbs are positioned horizontally, as though specifically aimed at the capture of dropping or jumping organisms. An interesting specialist, derived from orb-web spinners, is the retiarium spider, *Dinopis* sp. (Dinopidae), which spins an elastic net that it attaches to the closely appressed first and second legs of each side. The legs are held out before the spider with the net between them as it swings from a thread attached to a simple base spun on a low-growing bush. The net is stretched and used to snatch from the ground any crawling prey that approaches, or else it may be similarly employed to sweep flying insects out of the air. Two other members of the orb-web group (Araneidae) are more specifically oriented to predation on insects. Only the juveniles of the bird-dropping spider, *Celaenia kinbergi*, spin webs. The shape and colour of the adult makes it resemble a bird dropping, so birds ignore it if it remains motionless on bushes in daylight. At night, however, when visual deception offers no advantage, the spider becomes a hunter. Its robust legs are kept at the ready, and seemingly it emits an odour mimicking a lepidopterous sex pheromone, which lures male moths to its vicinity. In the Brisbane area its victims are the males of *Peripyrha sanguinipuncta* (LEPI: Noctuidae), but in other areas males of other noctuid species are attracted. Another remarkable araneid which has altogether abandoned orb-webs in favour of exploiting particular insects is *Dicrostichus furcatus* (the so-called bolas spider). This spider sits on leaves and dangles from one of its front legs a thread that terminates in a sticky globule. As in related species in Africa and the New World (= North and South America), glands on the spider's abdomen emit chemicals whose odours resemble sex pheromones, and lure male moths to its vicinity. Activated by the sound of wing beats, the spider whirls the sticky mace until it contacts

and captures the male moth. In Brisbane the prey are males of *Mocis frugalis* (LEPI: Noctuidae), but males of other species are captured in other areas. The lure emitted by both *C. kinbergi* and *D. furcatus* must therefore contain several components, because these predators are able to capture moths of an array of species. The flower spiders (e.g. *Diaea* spp. (Thomisidae)) have also abandoned web-spinning. They are so coloured as to blend into the background when lurking in flowers, and their evolution has oriented them to the capture of nectar- or pollen-seeking insects (McKeown 1963; Main 1976).

Among the Insecta predatory groups are more numerous than phytophagous forms (see Table 3.1). All active stages of Odonata and Mantodea are carnivorous, likewise most of the Neuroptera. So are the larvae of Megaloptera and Raphidioptera, the adults of Mecoptera and entire groups of the Orthoptera, Hemiptera, Coleoptera, Diptera and Hymenoptera. The Dermaptera include significant predators, such as *Chelisoches morio* (Chelisochidae), which can be important in pest ecosystems. There are many predacious thrips, and even the Lepidoptera, which are generally regarded as a prime example of a phytophagous order, contain forms which are voracious carnivores in the larval stage. Thus the caterpillars of *Batrachedra arenosella* (Batrachedridae) may exert a high degree of control over scale insects in orchards.

Mandibulate predators, such as *Paragryllacris* spp. (ORTH: Gryllacrididae) may simply seize insects and devour them progressively, despite continued struggling of the victim. Mantids, whose cryptic colours and posture usually enable them to escape notice until within striking distance, also consume the prey while it is alive and struggling.

Mandibulate feeding in the aquatic nymphs of Odonata (Fig. 17.11) is accompanied by the development of the labium into an extensible pincer for securing prey situated more than twice the head length in front of the larva. After 'firing', the labium is withdrawn back under the head, bringing the victim into contact with the other mouth-parts for consumption in more or less normal mandibulate fashion. A somewhat similar labial mechanism is found in the larvae of the beetle genus *Stenus* (COLE: Staphylinidae) (see pp. 623-4). Interesting modifications connected with mandibular predation occur in the larvae of Chaoboridae (DIPT), which have prehensile antennae used for holding prey. In the culicine mosquitoes of the tribe Toxorhynchitini the labial feeding brushes that are usual in larvae of the family are replaced by articulated spines used in catching and holding prey until the mandibles deal with it. Non-mandibulate predation occurs in adults of the dipterous family Dolichopodidae, which crush soft-bodied forms such as aphids between the labella. It is also a feature of the larvae of some muscoid Diptera which have a pair of mouth-hooks (modified maxillae) articulated with an internal cephalopharyngeal skeleton. By means of the mouth-hooks the larvae of some calliphorids, such as *Chrysomya rufifacies*, prey effectively on the maggots of other species, curling their tuberculate bodies around them to

enhance their purchase. Piercing mouth-parts are commonly used in predation. Many carnivorous bugs impale prey with their beak and inject salivary secretions along with toxins which immobilise the prey, and hyaluronidase, which rapidly breaks down connective tissue and allows other enzymes to penetrate quickly. The dissolved contents are rapidly withdrawn by the beak. Predation of this type is common among aquatic Hemiptera. Some of these have raptorial fore legs, and in the formidable fish killers, *Lethocerus* spp. (Belostomatidae (Fig. 30.55A), which may be up to 70 mm long, the powerful, incurved fore legs are armed with sharp claws with which they catch tadpoles, small fish and large insects. On land the assassin bugs, or Reduviidae, are the main group to hunt by impaling prey with their powerful curved beak. Bugs of the genus *Ptilocnemus* have a trichome on the ventral surface of the abdomen—a gibbosity flanked by dense tufts of setae, on to which opens a gland whose exudate is avidly sought by ants when the bug raises itself to allow them access. The secretion is narcotic and makes the ants easy prey. The details of this habit were described for exotic species, but it is stated that the Australian *P. femoratus* (Plate 3, K) also preys in this fashion. Some Miridae and members of other families of bugs are predacious without obvious modification of the phytophagous proboscis. This is true of the mirid 'freeloaders' on entomophagous plants (see earlier section), but it also occurs in other members of the group. For example *Tytthus mundulus* is an important predator on the eggs of the sugarcane leafhopper, *Perkinsiella saccharicida* (HEMI: Delphacidae) (Fig. 30.38A).

Predation on the wing is not as common in the Insecta as might be expected. The Odonata are the only order to have perfected this technique. Their legs are scarcely used in walking, but are strong, and serve as an efficient basket for capturing flying prey and feeding it to the mouth-parts. The other well-known aerial hunters are the robber flies (DIPT: Asilidae), which puncture captured insects with their stout beak and rapidly suck them dry (Fig. 3.22). Their legs, likewise, are little used for walking, but are efficient in capturing and holding prey. Some of the colonial vespid wasps pluck butterflies and other insect prey out of the air and plunge with it to the ground, where they sever the appendages to facilitate transport to the larvae in the nest they are provisioning, but they, and the Odonata and the Asilidae also 'glean' many victims roosting on bushes. Some Empididae (DIPT) also capture prey on the wing, but in this family prey is not merely food but often an adjunct to courtship. A captured insect is presented to the female before mating, but in some cases this may be self-protective because some empidid females are likely to devour their partner when mating is completed (Hamm 1933; McKeown 1942; N. C. E. Miller 1956; Spradbery 1973; Strong *et al.* 1984).

The ability to spin silk has evolved many times over in the Insecta, but quite remarkably, it is scarcely used at all by predators to construct snares as in the Araneae. Some fungus midges spin sticky snares that entrap small insects which are killed by oxalic acid secreted on to the web. In



Fig. 3.22 The robber fly, *Neoratus hercules* (DIPT: Asilidae), sucking the juices from a honey bee which it has captured on the wing; fly about 35 mm long.
[A. J. Nicholson]

Australia and New Zealand species of *Arachnocampa* have luminous larvae, which, in caves and protected places, spin snares of hanging threads studded with mucilaginous drops (Fig. 3.23). Otherwise, apart from rudimentary strainers spun by the aquatic larvae of a few chironomid midges, the only silken snares produced by Insecta are those of the larvae of Hydropsychidae (TRIC). These caddis larvae do not exhibit the case-bearing habit so common in the order, but spin wide-mouthed nets attached to plants or rocks that face into the current. The larvae live in the apex of the snare and harvest the organisms collected, sometimes engulfing portions of the net in the process. Animal prey is consumed, but diatoms are a more important component of the catch. From this aspect these nets also are strainers rather than snares. Thus, in spite of their great adaptability insects do not compare in any way with spiders in snare production. Spiders are so versatile that some of them produce up to five kinds of silk, including the sticky and dry silks that are so vital to the success of the vertical orb-web. In the Insecta these remarkable snares are paralleled only crudely by those of a few fungus midges (Common 1986; von Frisch 1975; Williams and Hynes 1973).

Very effective pitfall traps are constructed by the antlions, the larvae of the neuropterous family Myrmeleontidae. In dry, sandy places these larvae excavate conical pits by backing into the sand in a circular pattern and flicking away any material that elicits a jerking reflex by falling on the top of the head and long mandibles. In this fashion a conical pit is excavated, with the slope at the angle of repose of the sand (Fig. 3.24). When the pit is complete, the larva lies buried in the bottom, with its hooked jaws agape. The ubiquitous roving ants and other arthropods that tumble into the pit are usually seized immediately by the waiting predator. If, however, they seem to be making their escape, stimuli from the material they dislodge induces the antlion to pelt sand in their direction, so that, by direct hit or by creating landslides, the prey is brought down again into the bottom of the pit. A toxin and digestive juices are pumped into the victim's



Fig. 3.23 Snare of *Arachnocampa* larva (DIPT: Mycetophilidae). The larva is in upper background in a horizontal position; full-grown larva may be 30 mm long. [A. J. Nicholson]

body through channels between the coapted mandibles and maxillae. The liquefied contents of the prey are withdrawn through the same channels, and the exoskeleton is eventually flicked out of the pit.

Extraoral digestion, as exhibited by neuropterous larvae, also occurs in several families of Coleoptera, though the maxillae are not involved. In the Dytiscidae, the liquefied contents of the prey are withdrawn via the mandibular channel through which the enzymes were injected, but in the Lampyridae and Drilidae the channel is only used for injection of toxicant and enzymes, other mouth-parts harvesting the exuding juices.

Predation on behalf of offspring or brood is exhibited by worker ants and adults of pompilid, eumenine and sphecid wasps which themselves are usually largely nectarivorous. Some ants are omnivorous, when hunting on behalf of their young, but other groups may specialise on particular types of prey, for example, grasshoppers, leafhoppers, cicadas, flies, caterpillars or spiders. The victims are often paralysed so that they remain fresh for the progressively feeding larvae. In some groups the prey is killed outright, but nevertheless remains well-preserved because the injected substances perform a bacteriostatic function. Well-known in Australia are the policeman flies, *Sericophorus* spp. (HYMN: Sphecidae, Larrinae), which provision burrows with a number of paralysed Diptera. In hunting they pounce on crawling or resting flies, and appear not to effect any captures on the wing. Vespine wasps, themselves largely nectarivorous, chew up (malaxate) captured insects and feed them to the larvae in

the fabricated nests throughout the period of their development. In the process some of the juices may be utilised by the adults. [Froggatt 1917]

What amounts to a form of predation is practised by many small entomophagous Hymenoptera, particularly the Eulophidae and Pteromalidae. In these the ovipositor is used not only for inserting eggs into potential hosts but also for making feeding punctures for the withdrawal of nutritive body juices. Such punctures may greatly exceed in number those made for egg-laying, and, as they may also be availed of by male wasps as sources of nutriment, the drain on the host larva often results in its death. Leaf-mining larvae, such as those of the genus *Liriomyza* (DIPT: Agromyzidae) are particularly susceptible to this form of attack (Waterhouse and Norris 1987).

Insect defences against natural enemies are very varied. Apart from fast running in cursorial forms and evasive flight in winged ones, behavioural escape mechanisms include jumping, violent wriggling, dropping from food plants on threads (or just dropping), thanatosis (feigned death, involving varying periods of complete quiescence, chiefly to escape vertebrate predators) or autotomy (shedding of a seized limb). Structural specialisations to reduce risk of capture include slimy, waxy or flocculent coverings, urticating hairs, spiny processes, tough exoskeletons or coverings of caducous scales. Procrystis and mimesis (see later section) combine structural and behavioural adaptations. Chemical defences may involve sequestration of plant allelochemicals, which may be regurgitated, synthesis of specific toxicants or repellents, which may even be projected in jets, as in some phasmatids, cockroaches and heteropterous bugs, or dispensed from osmeteria or other special organs. Perhaps one of the most interesting defence mechanisms is the explosive discharge of quinones from the anal glands of the bombardier beetles (COLE: Carabidae, Brachininae) (see p. 614). However such a degree of sophistication is far removed from the self-defence mechanisms adopted by many larval thrips. With the help of their long and flexi-



Fig. 3.24 Antlion pits (NEUR: Myrmeleontidae), Katherine, N.T. In northern Australia the long dry season permits the larvae to construct pits in the open; but in the south they are generally under cover. Largest pits about 35 mm across. [K. R. Norris]

ble abdomen these insects smear liquid faecal material on sense organs and appendages of attackers, forcing them to withdraw and clean themselves before returning to the attack. Employing such a universal resource, with no special drain on the energy budget, is not as common as it might be among insects. Discrete defensive structures, which may also protect against the elements, include hard tests or scales, lerps or other firmly anchored shelters, retreats or tunnels of webbing, cocoons, tough portable cases reinforced with plant material and a large variety of other structures, as well as underground cells, burrows and tunnels in wood or other material. Certain aphids and leafhoppers escape the attentions of natural enemies by buying protection from ants in return for feeding them with copious supplies of honeydew. In defence of this resource the ants drive off the foes so effectively that their protégés may become severe economic pests. Some species of aphids have a non-reproductive 'soldier' caste whose members attack and impale predators threatening the members of their clone (see p. 454), and one encyrtid wasp, a polyembryonic parasitoid of a lepidopterous pupa, has a precocious, non-reproductive larval form that drives off endoparasites whose progeny might compete with its siblings (Brockmann 1986). Sterile soldier castes, employing chemical and mandibular defence methods, or perhaps passively plugging access holes with a sclerotised 'phragmotic' head, are a feature of the Isoptera. They and their nests and defence mechanisms are dealt with in Chapter 20, those of social wasps, ants and bees in Chapter 42, and the origin of eusociality in a later section of the present chapter.

PARASITISM, PARASITISATION AND PHORESY

Parasitism, as discussed in this section, is a form of *symbiosis* ('living together') of organisms of two species, the small dependent partner, or parasite, sometimes being known as a *symbiote*, and its relatively larger independent host as a *symbiont*. Kim (1985) defines a parasite as 'a symbiote that lives, throughout a part or the entire period of its life, in or on the host from which its food and other biological necessities are derived'. Insects such as bed bugs and blood-sucking flies which visit a host only to feed, are specifically excluded, and it also makes for clarity if we avoid the habit of referring to phytophagous insects as parasites of plants. Death of a host from attack by a coevolved parasite is not usual, the host living on after its symbiote has completed its life cycle, and taking on the burden of supporting its descendants. Many insects, however, have a special relationship with the host that involves their complete destruction of only a single victim in the course of their development. This is a different relationship from true parasitism, and the huge numbers of insects that have this habit have been given the name of parasitoids.

Insect Parasites of Vertebrates

Some insect ectoparasites are permanent (i.e., full-time) occupants of the body surface of their hosts. This is

true of all members of the Hemimeridae (DERM), Phthiraptera, Polyctenidae (HEMI), adults of some leptinine Leiodidae and some amblyopinine Staphylinidae (COLE), and Nycteribiidae, Streblidae and some Hippoboscidae (DIPT). Other hippoboscids, almost all Siphonaptera, parasitic Pyralidae (LEPI), Scarabaeidae (COLE) and members of other groups listed in Table 3.2 may leave the host for various purposes, such as ovipositing in its dung, but most are nevertheless regarded as true ectoparasites. A few insects that have commonly been regarded as ectoparasites, such as the Arixeniidae (DERM) and the Australian rodent-associated *Myotyphlus jansonii* (COLE: Staphylinidae) are now regarded rather as commensals.

Parasitisation by fleas, lice or hippoboscids may be directly debilitating to hosts, as is well known in domestic animals. On the other hand many species of insect ectoparasites produce little obvious effect. Most, however, are treated with active hostility if their host is physically able to reach them. Indeed man is the only animal ever known to welcome parasitosis, and some people regard lice as a necessary adjunct to a healthy life. Even the great Linnaeus suggested that children were protected by their lice from a number of diseases (Zinsser 1934). Selective pressures, resulting from attack by the host and the usually terminal consequences of falling off it, result in ectoparasites having hypertrophied claws and even pincer-like limbs. The mouth-parts may also be used to strengthen the purchase on the host, as in the rabbit flea, *Spilopsyllus cuniculi*, and the stickfast fleas of the genus *Echidnophaga*, which achieve more secure and enduring anchorage by means of their strongly serrated laciniae. In addition, other features of the life of ectoparasites alter or suppress various structures and elicit the development of new ones. Parallel evolution finds free rein among ectoparasitic insects, which tend to exhibit a readily recognisable facies (Fig. 3.25).

A common anatomical specialisation is the shortening and even the repressing of antennae, which, particularly in fast-moving insects such as fleas, reduces the risk of their being caught in hair or feathers. Eyes are frequently reduced or lost in permanent ectoparasites of endotherm vertebrates, having become unnecessary in host location and avoidance of enemies. In concert, olfactory and tactile capacities are closely tuned to life on the host, and sensitivity to gradients of CO₂ and temperature enhanced. Suppression of wings is common. The reasons for this are not obvious at first sight, but study of groups that contain volant ectoparasites helps throw some light on the problem. The Hippoboscidae includes many well-adapted parasites that are fully winged, but the wings tend to be rather leathery, as if the risks of abrasion were higher than normal. In spite of this, progressive severe wing wear commonly occurs. Moreover, some hippoboscids are caducous, shedding their wings after safe establishment on a host, as are species of Carnidae (DIPT) which are ectoparasites of birds. Severe abrasion also occurs to the wings of Pyralidae (LEPI) ectoparasitic on sloths. It can only be assumed that wings are generally a disadvantage to ectoparasites and that the pelage of endothermic hosts

Table 3.2 Significant food sources of the parasitic stages of ectoparasitic insects (modified from Marshall 1981).

Order	Family or Group	Blood	Feathers	Hair	Skin & Debris	Body Exudates	Other
DERM	Arixeniidae*				+	+	?insects
	Hemimeridae*				+	+	?vegetable matter
PHTH	Amblycera	+	+		+	+	various
	Ischnocera		+		+		
	Rhyncophthirina*	+					
	Anoplura	+					
HEMI	Polyctenidae	+					in possum nests
	Lygaeidae	+					
COLE	Leiiodidae			?	+	+	
	Staphylinidae				+	?	
	Scarabaeidae				+	?	
	Languriidae				+		
SIPH	All families (adults)	+		?		+	
						(1 sp. only, as larva)	
DIPT	Carnidae					+	host faeces
	Mystacinobiidae*						
	Hippoboscidae	+					
	Nycteribiidae	+					
	Streblidae	+					
LEPI	Pyrallidae					+	

* non-Australian group

is more unfavourable for their retention than one would expect. There would seem to be an advantage in ectoparasitic insects having highly flexible, blood-distensible wings, like those that give male Embioptera such mobility in their close-fitting silken tunnels, but none has developed such a mechanism.

Special features of many parasites, which have arisen independently in a number of groups are *ctenidia*, heavily sclerotised combs situated on various parts of the insect (Figs 3.25B, C). Traditionally, parasitologists have viewed these as devices to impede removal by the host during grooming, but they are never found to carry entrapped fragments of hair or feathers, and it is possible that most of them serve rather to protect vital flexible areas in the integument (Marshall 1981).

The food sources of most of the groups of insect ectoparasites of endothermic vertebrates are summarised in Table 3.2. Few actually feed on hair or feathers alone and commonly the diet is supplemented with body exudates, skin and skin fragments. In biting lice the fore legs may be modified to assist in scraping the skin, and others simulate the blood-sucking of their anopluran relations by biting their way into blood supplies in growing feathers. The Philopteridae (PHTH) ingest only feather fragments, a refractory food for almost all insects, but their digestion is assisted by commensal micro-organisms. Blood is a food more nutritious and uniform in quality than that available to the average phytophage, but it is poor in vitamins, particularly of the B group. This deficiency is made good by the activities of intestinal symbiotes in many haematophagous ectoparasites.

Although ectoparasites are put at risk from the grooming activities of the host, their mode of life largely frees them from the attentions of parasitoids and generalist predators. Thus they have no need to expend resources in

achieving warning or cryptic shapes and obliterative colour schemes or in adopting mimesis, as so many phytophages are driven to do. It is true that cryptic coloration finds muted expression in some bird lice that occur in pale plumage and have matching pale colours that make them less visible to the preening host (any dark species infesting the same host occurring on or near the head where the beak cannot reach them), but by and large vision is of secondary importance in attempts at disinfection. Thus, in ectoparasites, shape is dictated chiefly by the need to maintain a firm grip and defeat attacks by the host, and colours are basic, ranging from white through yellows and the predominant browns to almost black, and reflecting to a considerable extent the degree of sclerotisation. Lack of plant-generated pigments and precursors would limit their scope in any case, but selective pressures to put these to use would also be largely lacking.

Fleas. The laterally compressed body of fleas fits them better for more rapid movement through fur or feathers than would the squat body of most lice. Fleas are undoubtedly less host-specific than lice. Their stronger tendency to leave the host and the ability of some species to survive long periods without it probably contribute to their wider polyphagy. In most fleas loss of the power of flight is compensated for to some extent by a notable jumping ability, which, by a curious evolutionary economy, is conferred on them by modifications of some structures that were involved in flight in their ancestors.

Fleas, with one exception (see Chapter 38), drop their eggs freely, and in most species this occurs in a nest or lair where the vermiform, mandibulate larvae live in the detritus resulting from the activities of the hosts. However the organic matter consumed on the floor of the nest is often enriched by undigested blood passed in considerable quantities in the faeces of the adults. In this fashion

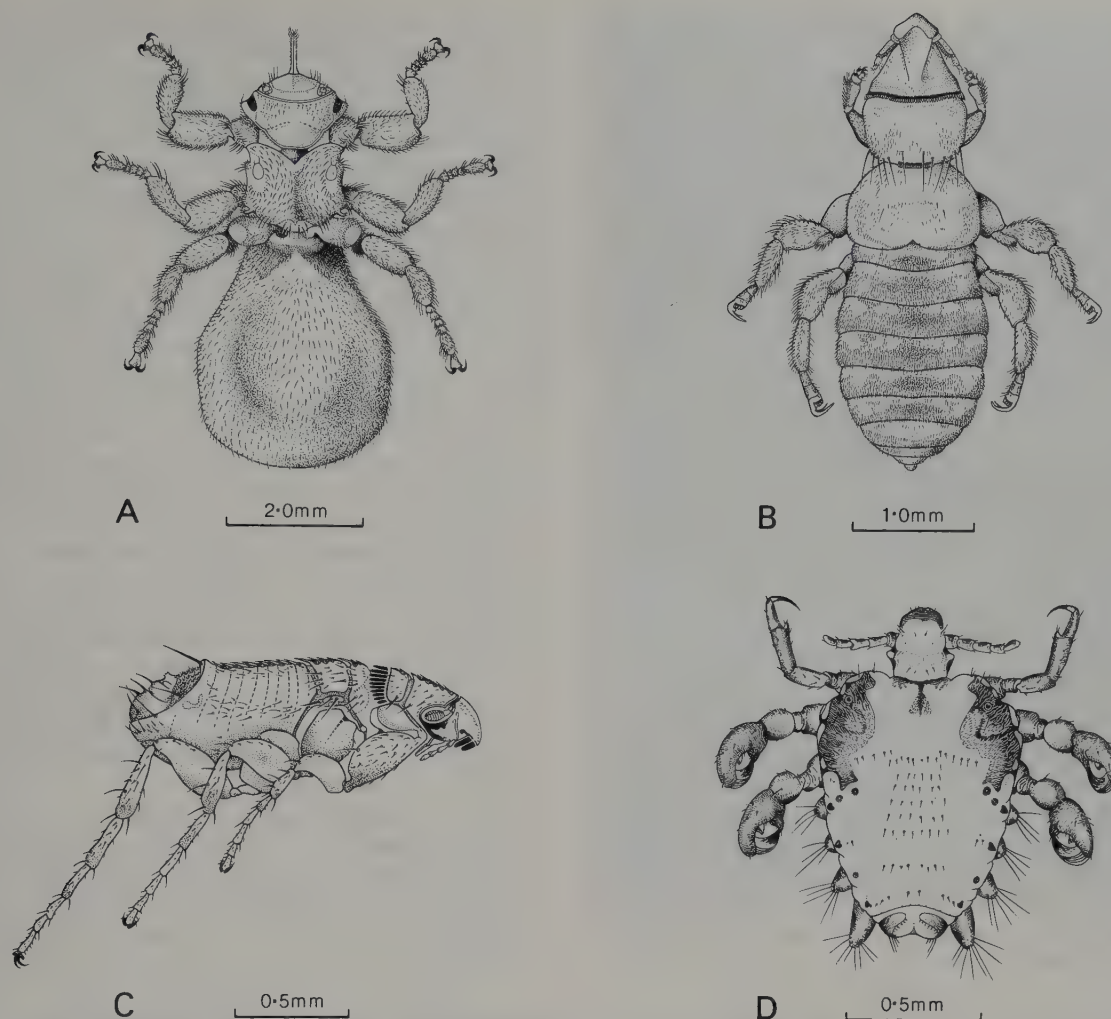


Fig. 3.25 Typical ectoparasites: A, *Melophagus ovinus* (DIPT: Hippoboscidae); B, *Adroctenes magnus* (HEMI: Polychenidae); C, *Lagaropsylla mera* (SIPH: Ischnopsyllidae); D, *Pthirus pubis* (PHTH: Pediculidae). [T. Nolan]

adult fleas exploit their parasitisation of an ample resource to feed their non-parasitic young. The degree of dependence on this source of food differs considerably between groups of fleas, but it may be very important. The avidity of the larvae of the rodent flea, *Nosopsyllus fasciatus*, for faecal blood, in fact, tempts description as an addiction. These larvae pursue the adult fleas, seeking to attach themselves near the anus. If successful, they drop off only when some undigested blood is voided, and promptly begin to feed (Kim 1985; Waage 1979b; Marshall 1981).

Adult fleas may remain in the pupal cocoon until the arrival of hosts in a long-deserted vicinity (see Chapter 9). A nice mechanism has been demonstrated in the phenology of the rabbit flea, *Spilopsyllus cuniculi*, which was introduced into Australia to speed the dispersal of myxomatosis (Chapters 9, 38). The reproductive cycle of this flea is so linked to that of its host through rabbit hormones taken up in blood feeds that a high proportion of fleas move from the pregnant doe into the floor of the breeding burrow when kittens are about to be produced.

Their feeding on the rabbit litter while it is nest-bound then assures their progeny of ideal conditions for completing their life cycle (Rothschild 1965). From this and examples of similar patterns in other species it is evident that host refugia are of critical importance to many fleas. In fact they are thought to have been vital to the evolution of ectoparasitism in general. Waage (1979b) postulates a Mesozoic origin for the important ectoparasitic groups, in which the nests of reptiles, then mammals and later birds provided the scenario necessary for the emergence of fleas, lice and some other forms. The significance of host nests in the evolution of fleas is underlined by the minor importance of this group on free-roving ungulates, which over most of the world are infested chiefly by a few non-specific fleas of little consequence to them. Fleas that have coevolved with ungulates occur chiefly in the Northern Hemisphere. In Asiatic USSR, for example, species of Vermipsyllidae infest horses, sheep, yaks and deer. Their eggs are dropped at random in the pastures, where the larvae feed on organic matter without the benefit of supplementation by blood from the host, and, not



Fig. 3.26 Eggs of pigeon body louse, *Hohorstiella lata* (PHTH: Menoponidae); eggs 0.9 mm long. [I. Roper]

surprisingly, only one generation is completed each year (Marshall 1981).

Lice. Response to texture of pelage and thermal and odour gradients on the host determines the life cycle, behaviour and predilection site of lice. Thus sheep are subject to infestation by three distinct species of lice, whose zones of attachment are almost always the trunk, face and legs respectively, areas having each a particular clothing of wool and/or kemp, or hair, and a characteristic regime of temperature and relative humidity.

Lice cement their eggs firmly to hair, wool or feathers (Fig. 3.26), and their newly-hatched young are able to feed directly on the blood or pelage and skin detritus or secretions of their host. The distribution of the head and crab louse on man is determined largely by hair texture, the latter, with its large pincers, seeking the coarser hair occurring on the pubes and in the axillae (Fig. 3.25d; Chapter 9).

Diptera. The ectoparasitic Diptera have become viviparous, the larva growing in a so-called 'uterus', until it is fully fed, when it is deposited either inside the refugium of the host or on its coat or plumage. Here the larva promptly glues itself to the surface and pupates. The feeding of the adults of these Diptera therefore provides nutriment for all life history stages. Like the lice, they

have no problem in host-finding, and, unlike fleas, they are highly successful in adapting to large, free-ranging ungulates, as shown by the fact that there are serious hippoboscids pests of domestic sheep, cattle and horses.

The larvae of bot flies (DIPT: Oestridae) are parasitic in the respiratory and nasal passages of mammals, the only Australian representatives being species of *Tracheomyia* which infest the tracheae of kangaroos. In this family it is the larva that finds itself with virtually inexhaustible supplies of food, and its feeding results in the pupa having very ample fat body deposits, which suffice for the nutrition and egg production of the adult and spare it the need to seek sustenance. In consequence of this evolutionary development, the mouth-parts of *Tracheomyia* are vestigial (Fig. 3.27), though they can be used to imbibe moisture to prolong survival. A similar nutritional pattern occurs in a number of other (exotic) families of Diptera whose larvae are parasites in the subcutaneous tissues or gut of mammals. The Old World screw worm fly, *Chrysomya bezziana* (DIPT: Calliphoridae), which occurs in Papua New Guinea, shows incipient development towards this condition. The larvae feed exclusively in wounds on warm-blooded animals, which nowadays are chiefly cattle, and, unlike carrion-feeding blowflies, the adults are able to lay an initial egg batch without protein feeding (Spradbery and Sands 1981).

Outside of the groups discussed above, Australian birds have no specialised insect parasites except the maggots of the fly *Passeromyia indecora* (DIPT: Muscidae), which are subcutaneous blood-suckers of the nestlings of 18 or more species of birds, chiefly of the order Passeriformes (Pont 1974).

No insect parasites of Reptilia are known in Australia, but interesting subcutaneous parasites of Anura are the blood-sucking larvae of *Batrachomyia* spp. (DIPT: Chloropidae). Fully fed larvae emerge from their burrows under the skin of frogs and pupariate in the soil. If not too heavily infested, the frogs may survive the parasitisation, little the worse for their experience.

Insect Parasites of Insects

The debilitating effects of insect parasites on some vertebrate hosts may be paralleled in the insect hosts of the

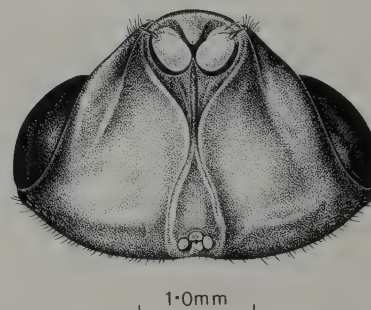


Fig. 3.27 Head of the bot fly, *Tracheomyia macropi* (DIPT: Oestridae) showing vestigial mouth-parts. [F. Nanninga]

Strepsiptera, but parasitisation by them has some additional consequences. In most species the degenerate larvae, male pupa and adult female lie in the body cavity of their hosts, which are usually Hemiptera or Hymenoptera. Here they displace internal organs, and parasitisation commonly causes anatomical peculiarities in the adult host. In Hymenoptera, for example, there may be changes in sexuality and in secondary sexual characteristics. The relevance of these changes to parasite biology, if any, is unknown (Spradbery 1973).

Apart from the three orders and minor groups already considered, parasites, as defined, are not prominent in the rest of the Insecta. The adults of the bee louse, *Braula coeca* (DIPT), are frequently found on queens and workers of infested honey bee colonies. These minute apterous insects solicit oral secretions from their hosts, and it is a moot point whether they should be regarded as true parasites. Other true insect parasites of insects are ectoparasites, such as the larvae of dryinid wasps (HYMN) (Fig. 3.28), epipyropid larvae (LEPI), which occur on immature leafhoppers, cyclotornid larvae (LEPI), which in the first instar are ectoparasitic on leafhopper nymphs, and chironomid larvae (DIPT) which infest nymphs of Ephemeroptera (Fig. 16.5). Some of these, such as first instar cyclotornid larvae, are said not to affect the survival of their hosts after detachment, and perhaps others do not. However there is a high probability that at least part of the exoskeleton of the host is damaged or deformed where the ectoparasite was feeding, and this is likely to reduce the chance of the host undergoing ecdysis successfully. Thus members of these groups probably conform somewhat uneasily with the formal definition of parasites.

Parasitoids

The paucity of true parasites in insect-insect relationships may be partly a reflection of the small average size of insects, which tend to be in about the same size class as the insect host they attack. So a different relationship has arisen, and, as mentioned earlier, many insects have become parasitoids contrasting with predators in consuming only a single host during their larval stages, and, unlike parasites, almost invariably bringing about the death of their host. They may feed externally or, more usually, inside the body cavity. Parasitoids that feed internally usually do not void their waste products during their trophic period, and they tend to leave vital organs such as heart and nervous system intact until the host is nearing death, when the remaining internal organs may be consumed. Pupation may take place inside the empty exoskeleton of the host, but, more usually the parasitoid forces its way to the outside through some weak point in the integument. If the host is not already dead the trauma of this exit usually ensures that it dies. Some hosts, such as large phasmatids, may survive the exodus of a comparatively small larva (e.g. DIPT: Tachinidae), and continue to live and reproduce, strictly placing the larvae as parasites rather than parasitoids.

The major insect groups containing parasitoids are the Hymenoptera and the Diptera, but there are examples in



Fig. 3.28 Larva of a dryinid wasp ectoparasitic upon a eurymelid nymph (HEMI). [F. Nanninga]

other orders, such as the Rhipiphoridae and the Meloidae in the Coleoptera. In the Hymenoptera, parasitoids predominate in the Stephanoidea, Megalyroidea, Ceraphronoidea, Trigonalioidea, Ichneumonidea, Evanioidea, Proctotrupoidea, Platygasteroidea, Cynipoidea, Chalcidoidea and Chrysidoidea, 11 of the 14 superfamilies in the Apocrita, into which the group is divided. In the Diptera the main families containing parasitoids are the Nemestrinidae, Acroceridae, Bombyliidae, Conopidae, Pyrgotidae, Cryptochetidae, Chloropidae, Sarcophagidae and, by far the most important, the Tachinidae.

The great majority of the hosts of hymenopterous and dipterous parasitoids are Coleoptera and Lepidoptera, but they also attack members of their own orders, a considerable number of Hemiptera and Orthoptera and members of other orders. Their attentions are not confined exclusively to Insecta, and there are insect parasitoids that attack Collembola, isopods, spiders, ticks, chilopods, millipedes, land and freshwater snails, land planaria and earthworms (Fig. 3.29).

Eggs of parasitoids may be laid on the surfaces of leaves that insects of the host species are likely to eat. This is a feature of some Trigonalidae (HYMN) which lay their small eggs (microtype) on or in leaf tissues of plants infested by their larval sawfly hosts. The site of egg laying may be more or less irrelevant if dissemination is by means of triungulins or other phoretic forms. Some parasitoids lay their eggs in those of the host. The Amiseginae (HYMN: Chrysididae) chew holes in the tough chorion of the phasmatid host egg to allow access to the interior for oviposition. Other forms insert the egg through the chorion, puncturing it with the ovipositor during the process. In some insects that lay into insect eggs the early instar larvae do not become aggressive feeders until the host egg has hatched and larval development has advanced somewhat. Eggs laid on the bodies of hosts may be stalked or sessile. Stalks pass through the cuticle and serve to anchor the egg in the oviposition puncture. Sessile eggs that are firmly attached to the integument may give little external evidence of the invasion of the haemocoel by the parasite, as it often bores directly in through the small area of attachment. Long slender



Fig. 3.29 Earthworm being consumed alive by the 3rd-instar larva of the blowfly, *Calliphora tibialis* (DIPT: Calliphoridae); arrow indicates approximate position of head of larva inside tissues of worm; remains of worm 55 mm long. [C. Lourandos]

ovipositors evolved for seeking hosts deep in plant tissue may require the egg to undergo gross deformation during its deposition.

The term parasitoid is widely used, though many entomologists use the term parasite (e.g. Chapter 42) to cover them as well as true parasites. There are certainly grey areas, as relatively few people seem to apply the term parasitoid to egg parasites or the term hyperparasitoid to insects that attack other insect parasitoids inside their hosts. Hyperparasitoids occur principally in the Hymenoptera. Even though they feed secondarily, the end result is the same, the death of the host. Some species can perform the role of primary parasitoid on some hosts and hyperparasitoid in others, according to circumstances.

Other Natural Enemies of Insects

Apart from attack by other insects, the Insecta are subject to parasitisation by a variety of other organisms. Many mites (ACARINA) are ectoparasites (Fig. 3.30). A common form attacking soft-bodied larvae is *Pyemotes herfsi* (Pygmephoridae), which is of some importance in insect population regulation. Other non-insectan parasites of insects include helminths of various phyla, fungi (a range of genera in this group being specific to insects (Fig. 3.31)), Protozoa, bacteria, Microsporidia and viruses of various types. Transmission of micro-organisms is frequently by contact or oral consumption of spores, but parasitic mites may spread some during their feeding, and so could midges that suck insect blood. Thus a minute midge, *Forcipomyia fuliginosa* (DIPT: Ceratopogonidae) has been found sucking the blood of the larva of *Antimima cryptica* (LEPI: Notodontidae) in W.A. Such midges are common and widespread in this continent, and close relatives of them are well-known to attack insects in other countries. They may well be important vectors of insect diseases (K. M. Moore 1958).

Phoresy

Many organisms are found attached to members of other species in such a fashion that it is obvious they are not drawing sustenance from their patron, but are using it purely for purposes of transportation. This phenomenon is known as *phoresy*. The term does not apply to a very casual relationship, as when, say, a thrips is temporarily entangled in the vestiture of a hirsute foraging bee, nor does it seem appropriate to use it to describe the attachment of lice to blood-sucking flies, that is sometimes observed, when this may be no more than a consequence of accidentally seizing a seta rather than a hair. Rather the term is used to describe a regular relationship. Many mites, common in dung and refuse, routinely attach themselves to house flies and allied forms, sometimes even undergoing a metamorphosis into a special, non-motile dispersive stage (hypopus) when attached. First instar insect larvae may utilise adult insects as vehicles to reach the young they parasitise. Thus planidia of some Rhipiphoridae (COLE) attach themselves to bees or wasps, and triungulins of some Meloidae (COLE) likewise attach themselves to flower-visiting bees to gain access to the larvae in nests. Triungulins of Strepsiptera that parasitise larvae of wasps and bees are likewise phoretic upon the adult insects (Sweetman 1936).

Certain small beetles of the genus *Onthophagus* (COLE: Scarabaeidae) (formerly grouped in the artificial genus *Macropocopris*) are phoretic upon macropodids. They cling to the fur of wallabies near the anus, where they are strategically situated to mount faecal pellets as they are extruded, ride them to the ground, and commence immediate burial. This practice obviates the need for them to make wide-ranging searches for a pabulum for their larvae in a terrain where such materials, already severely depleted of moisture by the xeric adaptations of the donor, rapidly desiccate further if left on the soil surface.

COLOUR AND FORM, MIMICRY AND POLYMORPHISM

Very important in offence and defence are the devices by which insects advertise their distastefulness, conceal their edibility, or dissemble their aggressive nature. Adapt-

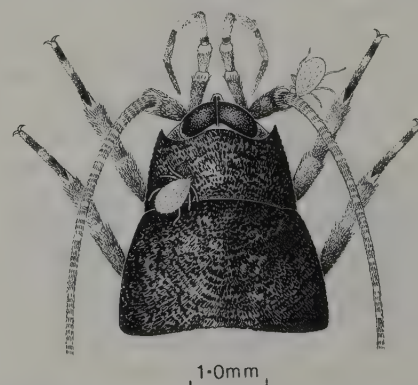


Fig. 3.30 Larval erythraeid mites (ACARINA) ectoparasitic upon *Allomachilis froggatti* (ARCH: Machilidae); mites about 0.75 mm long. [F. Nanninga]



Fig. 3.31 A bush fly, *Musca vetustissima* (DIPT: Muscidae), killed by the fungus *Entomophthora muscae*; conidiophores have protruded through the intersegmental membranes and thrown off the surrounding deposit of conidia; length of fly 5.5 mm. [J. P. Green]

ations based on colour and form are responses to predation by animals which hunt by sight, rather than by smell or other senses. Colour vision in birds, primates and some reptiles must be an important factor in bringing about mimesis and warning coloration, but many animals without colour vision must nevertheless be able to recognise bold, contrasting patterns, thereby adding to the selective pressures for anticrypsis. Rothschild *et al.* (1984) demonstrated that warning colours in insects are usually associated with discouraging odours, broadening the spectrum of possible predators contributing to the selective pressures.

Crypsis

The combination of colour, structure and behaviour that aids concealment of an animal is called *cryptic*. If the crypsis (Rothschild 1979) aids the insect to escape the attentions of a predator, it is known as *procrptic*, an instance being the stick-like appearance and posture of many Phasmatodea. Procrptic insects may be so coloured and shaped that they merge into the background which they commonly inhabit, and they generally contribute to the illusion by appropriate behaviour. Some moths (e.g. ennomine Geometridae) have intricate, disruptive wing markings of wavy lines, which blend with the bark of tree trunks where the moths rest with the wings pressed to the surface, and with their pattern aligned with the pattern of the bark (e.g. Nicholson 1927, Plates 13, 14). Procrpsis may also be brought about by resemblance to some object which is repugnant or uninteresting to the predator. Thus the larvae of the butterfly, *Papilio aegaeus* (LEPI: Papilionidae), are olive black with white markings and strongly resemble bird droppings, and their sedentary daytime habits contribute to the deception. Larvae of geometrid moths commonly resem-

ble twigs of bushes on which they live, and their posture and immobility heighten the resemblance. The larvae of the moth *Anisozya pieroides* (LEPI: Geometridae), which feed on *Acacia*, have the body segments broadly flanged so that they resemble the leaflets of the host plant. Various weevils, leafhoppers, and other forms also resemble parts of the plants upon which they live and feed, and are behaviourally adapted to heighten the procrptic advantage that this confers.

When concealing coloration and behaviour enable a predator to approach potential prey without being detected, the phenomenon is known as *anticrypsis*. It is exhibited by mantids, which, according to species, tend to look much like twigs, leaves, or the bark surface on which they usually lurk while awaiting the approach of prey. It is likely that this adaptation also enables the mantids to escape vertebrate predation, and is consequently as much procrptic as anticryptic (Dendy 1929).

An interesting sidelight to procrpsis is that many insects exhibiting it have, in effect, a second line of defence. If they are forced to break their cryptic posture by the close approach of a predator, they may startle it by suddenly moving their appendages so as to display a normally concealed pattern of bright colour. For example, if mantids are provoked until they are forced to move, many species then briefly exhibit blazes of colour on the wings, or on the inner surfaces of the femora. A third line of defence may also be employed. For example the female of the mountain grasshopper, *Acripeza reticulata*, is quite inconspicuous in repose, but, when disturbed, it raises its tegmina, and displays a strikingly colored, banded abdomen (Plate 2, L), but if provoked further a yellow bladder is protruded from the dorsal surface of the cervical membrane. The extrusible, often forked, brightly colored organs that occur on the prothorax of the larvae of some Papilionidae, Notodontidae, and also elsewhere on the body in other Lepidoptera have a disconcerting effect, but some of them at least also disperse volatile repellent substances (Crossley and Waterhouse 1969).

Aposematism

In addition to chemical deterrents of the above type, many insects have strongly distasteful or toxic qualities, and advertise this with bold patterns and flamboyant colours. So do many insects with potent stings and some with a powerful bite. Patterns of this type are known as *aposematic*. They are widely displayed by the formidable wasps of the families Pompilidae and Vespidae, which, by injecting potent toxins, are capable of aggravating many times over the mechanical effects of puncture with their stings. The bright colour patterns adopted by distasteful and dangerous insects serve as a warning to potential predators, which quickly learn their lesson when naïve and venturesome, and seldom require many exposures to teach them to associate the visual warning with pain or discomfort. Consequently, relatively few individuals of an aposematically marked species have to be sacrificed before its members achieve significant protection from attack by an individual predator.

Müllerian Mimicry

In some cases groups of distasteful or injurious species exhibit rather similar patterns of warning coloration, which further reduces mortality necessary to educate predators. This standardisation, resulting in economy in the lives of maleficent insects, is known as Müllerian mimicry (after the German zoologist Fritz Müller, 1821–1897, who first recognised the nature of the phenomenon). Some other word than mimicry might be preferable in this case, as it is sometimes far from clear whether any particular species has the status of a model.

Batesian Mimicry

A remarkable consequence of aposematism is mimicry proper, generally described as Batesian mimicry after the English naturalist H. W. Bates (1825–1892), who first called attention to it. In the development of Batesian mimicry, processes of natural selection result in individuals of a species or morph that is devoid of distasteful or injurious properties but highly acceptable as food for predators, deriving protection by mimicking the colour, form and behaviour of an aposematically coloured and patterned maleficent insect (Plate 6). To be successful in such deceptions, a mimetic species must be much less common than the model, otherwise the protection breaks down because the predators find a sufficiently high percentage of palatable insects amongst their 'warningly' colored prey to make an odd unpleasant experience tolerable.

A number of Australian species of Diptera, particularly of Syrphidae, Asilidae, Bombyliidae and Conopidae exhibit faithful mimicry of stinging wasps (Plate 6, Fig. 3.32, and Nicholson 1927). The colour patterns are reproduced with great exactitude, and the 'waist' of the wasp is often simulated either by actual constriction of the body or by countershading so as to give the impression of constriction. The long antennae of these forms are held as in the wasps, and sometimes the continuous palpation that many wasps perform is faithfully simulated. Wing-flicking, which is often a characteristic of foraging wasps, is also often imitated.

Other wasp mimics occur in the long-horned beetles, whose antennae afford a good starting point in the imitation of a wasp (a basic general resemblance of model and mimic is presumed to be a prerequisite for the commencement of evolution towards more detailed resemblance (Rothschild 1979)). This is heightened by the great abbreviation of the elytra, which in the non-volant insect con-

vey the impression of the bulky thorax of the wasp. They cover the bases of the permanently extended hind wings, which simulate well the shiny, fumed wings of wasps.

The aposematically colored orange and black beetles of the genus *Metriorrhynchus* (COLE: Lycidae) (Plate 6, A) which are distasteful to predators, are abundant in Australia, and serve as models for a wide variety of non-distasteful (Batesian) mimics, especially in the Coleoptera and Lepidoptera. Warning odour components, bitter principles and anti-feedants have been found in extracts of the common *M. rhipidius*, confirming its status as both model for Batesian mimics and a member of a Müllerian guild (Moore and Brown 1981; Rothschild *et al.* 1984).

Many ants are distasteful, or else they secrete repugnatorial fluids, or are capable of stinging or biting severely, and so it is not surprising that ant mimics are common. For instance, both immature and adult stages of the bug *Daerlac tricolor* (HEMI: Lygaeidae) mimic the ant *Dolichoderus doriae*, though the deception is produced by quite different anatomical modifications in the nymph and adult. Other ant mimics occur in the Phasmatodea, Orthoptera and Lepidoptera, and a number of spiders mimic ants closely, usually with the anterior pair of legs simulating the antennae, and the body nicely shaped or shaded to give the appearance of the constricted waist of the ant.

Aide-Mémoire Mimicry

In addition to the classic forms of mimicry, aide-mémoire mimicry has been described, a somewhat different sort of 'bluff' by which insects exploit behavioural patterns and general physical appearance to convince predators that they are likely to experience a repetition of some previous unpleasant event if they attack. Such warning may be issued in the form of display of bold colour patterns, even without shape imitation, by repeated forward movement of the tip of the abdomen to simulate stinging, display of pseudostings, adoption of patterns or structures resembling dangerous animals (even vertebrates), emission of buzzing sounds to fake the noise of formidable Hymenoptera and other means. Aide-mémoire mimicry does not require that its exponents be mistaken for particular species of noxious or dangerous prey. It is sufficient for the aggressor to be forced to recall the attributes of such species and the unpleasant consequences of some previous attack on creatures exhibiting such characteristics. Aide-mémoire mimicry is often reinforced by the presence of chemical defences, in which it is more closely akin to Müllerian rather than Batesian mimicry (Rothschild 1984).

Colour Morphs, Colour Change and Phase Polymorphism

Chance variation between individual insects in colour and form is the basis for the selection of the various forms of concealment and mimicry. There are, however, other forms of colour and anatomical variation which are not involved in or produced by such processes. For example there may be genetically determined colour morphs, and



Fig. 3.32 Wasp-mimicking syrphid fly, *Microdon variegatus*.
[From a photo by A. J. Nicholson; F. Nanninga]

phase polymorphism due to the influence of ethological and phenological phenomena. These are particularly important in the Orthoptera (Chapter 24). Phase polymorphism also occurs in Phasmatodea (Chapter 25) and Lepidoptera (Chapter 41). The term kentromorphism refers specifically to differences between phases in colour and structure, irrespective of behavioural and physiological differences. It is useful as a taxonomic term. Remarkable short term reversible colour changes occur in some Orthoptera (Chapter 24), and physiological colour changes occur in some Odonata (Chapter 17).

Cyclical Polymorphism

Cyclical polymorphism (cyclomorphosis) is a phenomenon that may result in many types of insect morphs, differing in anatomy, coloration and physiology occurring within a species. It is particularly a feature of many species of Aphidoidea (HEMI). Quite different forms of aphids may appear in different generations as the annual cycle proceeds. In some species this may result in more than 20 different forms of the same species occurring in the course of a year. The forms differ from one another in a variety of anatomical and physiological features, some being apterous, others fully winged, some parthenogenetic and viviparous, others sexually reproducing and oviparous. There are variations in colour, in the structure and relative length of appendages and in numerous other anatomical features. Cycles may be further complicated by obligatory alternation of the infestations between two entirely unrelated host plants, on each of which distinctive forms of aphids may develop. One form of annual cycle, which occurs in the introduced *Myzus persicae*, is described in Chapter 30 and illustrated in Fig. 30.20.

SOCIAL INSECTS

Truly social (eusocial) insects are those that form colonies comprising one or a few reproductive females and an assemblage of sterile progeny who assume the burdens of maintenance, extension and defence of the nest, and the provisioning and care of the brood. The order Isoptera (Chapter 20) is comprised entirely of such eusocial species, and there are many in the Hymenoptera (Chapter 42). The origin of eusociality and its biological significance have been the subject of much debate, but examination of existing insects reveals a number of pointers (both positive and negative) that may indicate possible evolutionary pathways to the superorganism, as the eusocial insect colony is sometimes described.

Protection of the eggs is common throughout the Arthropoda, occurring in myriapods and entognathous hexapods, as well as in a number of true insects. It is common in the Heteroptera (HEMI), a good example being afforded by the large bug, *Tectocoris diophthalmus* (Scutelleridae) (Fig. 30.20), the female of which guards her egg batches until hatching occurs. Bagnall (1915) reported that the female of a species of thrips, *Elaphrothrips brevicornis* (THPT: Phlaeothripidae), mounts guard over her egg batch laid on a leaf, and Anon. (1979) describes how a butterfly, *Hypolimnas antelope*

(LEPI: Nymphalidae), maintains guard over her eggs, even in the face of vigorous disturbance, until they hatch and the larvae disperse. Other forms show a slightly more advanced level of maternal care. The females of many Embioptera, for example (Chapter 26), guard not only the eggs, but also the 1st-instar young until they have spun their own tunnels. In the Coleoptera, bark beetles of the weevil subfamilies Scolytinae and Platypodinae, some species of Silphidae, and mated pairs of Passalidae, show some care for the young. The females of certain sawflies, such as *Pseudoperga lewisii* (HYMN: Pergidae) (Fig. 3.33), also extend their protection to the young larvae as well as to the eggs. Females of many Dermaptera (p. 363) tend their eggs in burrows, moving them around extensively during development, and standing guard over the young for a week or two after they hatch.

Apart from extension of parental care, what features in a candidate insect group pave the way to or prevent advancement to eusociality? Michener and Michener (1951) quite reasonably suggested that a special type of nervous system is a prerequisite for the evolution of eusociality, a brain that is capable of dealing with the complex activities required, and also of the considerable learning that is necessary to complement the inevitable inbuilt patterns of behaviour. Colonial insects also need to have efficient mandibulate mouth-parts to enable them to perform the nest duties, including structural work and feeding and tending the brood. From this aspect there need be no surprise that egg-guarding forms in the Hemiptera, Thysanoptera and Lepidoptera have not given rise to eusocial forms, or that the large order Diptera includes no members with any trace of sociality. The Embioptera have appropriate mouth-parts, but their fore legs are so strongly specialised for the almost continuous production of silk as to be unsuited to other nest duties. Some insects with unmodified legs are otherwise unsuitable for eusociality; for example, the Phasmatodea, whose clumsiness, coupled with evolutionary investment in defence measures involving cryptic posturing, thanatosis and autotomy rules them out of any role as caring parents. At first sight



Fig. 3.33 Female of *Pseudoperga lewisii* (HYMN: Pergidae), brooding over her newly hatched larvae. Female 16 mm long. [A. J. Nicholson]

the Dermaptera might appear to be suitable candidates for eusociality, but the maternal solicitude for the eggs and young nymphs is superseded after a few weeks by cannibalistic tendencies. Carnivory in the adult form or specialised legs would tend to rule out any group, and so would aquatic larvae in insects with terrestrial adults. It is not difficult to proceed through the insect orders in this fashion, identifying features that preclude the members from becoming eusocial, but it would be difficult for anyone to say why the huge order Coleoptera, with its diverse mandibulate members, totally lacks such societies. The family groups of the Passalidae, involving pairs of adults feeding their young with chewed wood throughout their larval life, is the highest development of sociality in the Coleoptera, but these families are not eusocial.

Subsocial Blattodea (Chapter 19) may depict for us a stage in the evolution of the Isoptera from their blattoid ancestors. For example, various Australian roaches of the genera *Panesthia* and *Macropanesthia* (BLAT: Blaberidae) live in family communities comprising pairs of adults and their immature young. The roaches harbour in their guts flagellate Protozoa akin to those that assist in wood digestion in the termites. An even more advanced form of subsocial behaviour is shown in the northern hemisphere woodroaches, *Cryptocercus* spp. (BLAT: Cryptocercidae), best known from studies on the North American *C. punctulatus*. These roaches also live in family groups consisting of a mated pair and a number of nymphs, almost always of one age group. The parents usually raise only a single brood in their lifetime, nourishing them by trophallaxis on hind gut fluids for at least three years, perhaps even for five or six years, until they are near their final moult. The feeding process infects the nymphs quite soon after hatching with flagellate Protozoa (again akin to those in termites) and other micro-organisms that assist in the digestion of wood, and it keeps them infected throughout nymphal life. A wood diet is of extremely low nutritive value, and it is particularly poor in nitrogen. Consumption of cadavers and other organic debris does something towards improving the nitrogen status of the adult food and of the hind gut fluids, but in spite of such measures the food is still of low value, which is reflected in the long nymphal period. The habit constitutes a severe drain upon the reserves of the parental pair. They not only have to feed the brood, but must also defend the nest and attend to its sanitation, and repair and extend galleries. A newly founded termite colony is also a subsocial unit. As in *Cryptocercus* it is also under nutritional stress, the body reserves of the founding pair being severely depleted before the first-raised brood is able to make a contribution to colony maintenance. Therein lies an essential difference between the termite colony and the *Cryptocercus* subsocial unit: in the roach the burden of maintaining the colony is not picked up by the next generation.

Cryptocercus itself is not to be viewed as a relict ancestral termite, since it is apterous, and it is inappropriate as a direct ancestor in various other ways, but its colonies can be viewed as representing a grade in the evolution of the superorganism. The adults certainly adumbrate ter-

mite eusociality in their care of brood and nest, but, in addition, several features of nymphal behaviour reflect possible steps along the same pathway. The nymphs exhibit a primitive means of communicating alarm when they encounter an intruder in a gallery of their nest. They run in search of nestmates, and, by a mechanical jerking behaviour, impart their sense of alarm to the adults, either directly or via siblings which they have aroused. No chemical message is involved, because the adults eventually go in search of the invader, waving their antennae in obvious preparation for its physical detection, and then they often enter the wrong tunnel. Another interesting parallel to termite organisation is that young nymphs groom the adults, probably in the course of soliciting hind gut fluids, but exhibiting a habit that would obviously pave the way for the establishment of reproductive dominance by hormone administration.

The important feature that is lacking in *Cryptocercus* families is that the progeny do not carry out effective nest duties. According to Seelinger and Seelinger (1983) advanced nymphs of *Cryptocercus* may participate in defensive operations against nest invaders, and they also join the adults in digging frass into breaches that have been made in the nest wall, so that, albeit very late in the life of the nymph, we see the beginnings of participation in nest duties. However, the really significant nest duty is feeding and care of the brood, which clearly cannot occur if the young are all of the same age group, as in *Cryptocercus*. To achieve this, up-grading of adult nutrition would be necessary, so that reproduction could be resumed. This could be achieved by refinement of the relationship with gut symbionts. Assumption of care for younger brood by advanced nymphs would then have two important effects. The trophallactic contributions made by the older nymphs to their younger siblings would halt their own accumulation of resources, and so prevent them from becoming reproductive, and at the same time the adult pair, being freed to accumulate extra reserves, would be able to reproduce even more effectively. This is a simple nutritional basis on which the evolution of eusociality could be advanced. However, in all termite societies the outcome of any such predisposing situations has been stabilised by the superimposition of other mechanisms, including the circulation of hormones that establish reproductive dominance (Nalepa 1984, 1988; Seelinger and Seelinger 1983).

Great longevity is essential to the reproductive success of *Cryptocercus*, and it is also an essential feature of all eusocial insects. Termite kings and queens (the founding pair) are known to live for decades. In this, and in a combination of appropriate anatomical and behavioural characteristics, trophallaxis and other features, termite eusociality has had its foundations, and in this group it is important to stress the cohesive force lent by the low nutritive value of their chosen food, wood, in enforcing long associations between family members.

The last factor has played no part in the origin of the eusocial Hymenoptera, whose food sources, in contrast with those of termites, have resulted in many of them retaining their powers of flight. Notable exceptions are

the ants, whose queens all undergo de-alation, the more highly evolved genera mobilising the flight muscles into fat body, from which larval nutrients are drawn. A fundamental difference between termite societies and those of eusocial Hymenoptera is that, in the latter, the males play only a reproductive role and are often quite ephemeral, whereas members of termite societies, though almost all sterile, may be basically either female or male. It is thought that the presence of a sting in the females of most Hymenoptera that have given rise to eusocial groups gives them an advantage for conversion to neuters. The males could perhaps be converted to efficient workers, but the females are equally suitable and moreover come ready equipped for duty as a soldier as well. This is an alternative denied to termites.

A broad section of the Hymenoptera must have constituted ideal ancestors for the evolution of eusociality because it has arisen in three families and along several clearly separate evolutionary pathways. Non-progressive nest provisioning by solitary Hymenoptera is an ancestral foundation for eusociality, and a wealth of existing forms makes it possible to reconstruct the course of its development through progressive provisioning to the enduring superorganism (Brockmann 1986). As in termites, longevity is a vital feature in the reproductive females. Queen bees may remain as heads of colonies for several years, though seasonally they may lead swarms, part of the colonies they dominated, to new sites, and the sole or chief reproductives of social wasps must survive for a year at least to ensure the continuity of their colony. Ant reproductives may be very long-lived, vying with termites in this regard, and like them, surviving severe nutritional stress and depletion of fat body tissues in raising their first workers.

It is considered that there have been two different pathways to eusociality in wasps, with the end result being much the same (Brockmann 1986). One has been via parasociality, involving joint nesting by unrelated females. The female wasps cooperate in the construction and care of the nest, but in the initial stages the relationship is only quasi-social, each female maintaining her own brood. Eventually strong reproductive dominance may arise in such associations, resulting in sterility in all but one female, the remainder tending her brood in a truly eusocial community. The second pathway to eusociality in wasps has been through subsocial communities, a family relationship involving nest sharing between long-lived mothers and their daughters. This too may lead to joint provisioning of the same brood cells and co-operative nest care and defence. Eventually the development of a strong reproductive dominance by the mother reduces the daughters to the status of workers, resulting also in a eusocial community.

The maintenance of reproductive dominance and caste formation, where it occurs, involves a complex web of genetic factors, chemical communication, hormone administration and dietary manipulation. The biological advantage accruing to the resultant superorganism is not always clear, and speculation and discussion on the topic have filled many volumes. Some biologists consider

that the protection afforded by the nest, and its defence by expendable neuters, gives a eusocial insect species an advantage, but the surrounding countryside is often swarming with solitary species, thriving without these safeguards, and the colonies themselves often harbour enemies in plenty. For example, inquiline—tolerated spongers—are frequently numerous in termite and ant colonies, which may also be infested by predators that attack brood or even all stages, while colonial wasps and bees are frequently plagued by parasitic kindred species, whose young they unwittingly rear, and ant colonies in some countries fall victim to slave-making relatives. Stability of ecoclimatic conditions in the nest is also cited as an advantage of eusociality, but the inquilines, parasites and predators also find the conditioned atmosphere congenial. Perhaps the reproductives of eusocial insect colonies can be compared with the adults of numerous vertebrate species which orient their reproductive activities in such a fashion that their own genome is more likely than others to be passed on to succeeding generations. However, the subtle chemical manipulation of the adult eusocial insect leaves the courtship display and real or ritual fighting of male vertebrates far behind.

In recent years a new twist has been given to the topic by the discovery of eusociality in the naked mole rats of the species *Heterocephalus glaber*. These long-lived East African mammals form underground colonies, with specialised reproductive 'queens', whose hormones, dispersed throughout the colony via urine voided in latrine chambers, largely suppress breeding in other colony members, which are then available in various physical and behavioural types, for the maintenance and defence of the colony (Gamlin 1987).

MIGRATION

by R. A. FARROW and V. A. DRAKE

All insects exhibit a capacity for movement at some stage of their life cycle. Movement allows an insect (1) to maximise its chances of survival and its reproductive success by exploiting hosts and habitats which vary in quality with time and from place to place (Dingle 1972; Farrow and Daly 1987; Gatehouse 1986; Southwood 1962, 1977; Taylor and Taylor 1977), and (2) to escape, at least temporarily, from natural enemies and disease. In many species, the appetitive (or 'trivial') (Southwood 1962) movements associated with the daily activities of locating food, mating, sheltering, and avoiding enemies, achieve a degree of local dispersal (i.e. a redistribution of the population) that is sufficient to ensure the successful development of a subsequent generation. Other species undertake more sustained movements that transport individuals between habitat patches or geographical regions. These often involve a temporary suppression of appetitive behaviour and station-keeping responses (Kennedy 1961a, 1985), and are termed migration (Johnson 1960, 1969).

Entomologists now generally accept a broad definition of migration that includes single-direction and lifetime

displacements as well as the outward-and-return or closed-loop movements that are more commonly undertaken by vertebrates (e.g. birds) (Baker 1978). Migration comprises both behavioural and ecological processes, and this has led to some debate over how the term should be used (Kennedy 1985). Ecologists have emphasised that the outcome of migration is the displacement of populations in a way that enables them to exploit favourable habitats that are spatially separated (Taylor and Taylor 1983). Behaviourists prefer to define migration as a persistent, straightened-out movement which results in ecologically significant displacements between generations (Gatehouse 1986; Kennedy 1961a; Southwood 1981). Sustained appetitive movements that may result in colonisation of new habitats (Jones *et al.* 1980) would not be considered migratory according to the latter definition, even though, as in the case of locust swarms (Kennedy 1951), distances of several hundred kilometres may be covered over the insects' lifetimes.

Migratory species vary in size from the tiniest microhymenopteran, with a mass of less than 1 mg, to locusts with a mass of over 3 g. The smaller species usually outnumber the larger (Farrow 1982c). Migration most commonly occurs by flight during the winged, adult stage of the insect's development. Less frequently, it is undertaken by the first instar, which produces a silk thread on which it is carried aloft by upcurrents. Some very small wingless insects are able to migrate in the air without the use of a silk thread. Migration is almost always actively initiated and sustained, although its termination, and the direction and distance of displacement, are often controlled by environmental factors. Nocturnal migration is initiated at dusk with a take-off flight in which the migrants ascend under their own power to altitudes of at least 100 m, and sometimes to 1–2 km. The time of take-off is related to changing light levels and is earlier on overcast evenings. A few species of nocturnal migrants also make brief flights in the early morning following a take-off during the period of changing light levels at dawn (Riley *et al.* 1987). Daytime migration is less synchronised but typically begins 1–2 h after dawn as temperatures rise above the migrants' flight thresholds. It also involves deliberate launching into the air and, in the case of winged insects, an active ascent flight.

Many economically important pests of agriculture are migratory (Farrow and Daly 1987; Gunn and Rainey 1979; Joyce 1983; Sparks 1986). Other migrants are not directly damaging but are vectors of plant, livestock or human diseases of major economic and social importance (Kay *et al.* 1987; Murray 1987b), or, like the bush fly *Musca vetustissima* (Hughes and Nicholas 1974), are nuisance rather than economic pests. Movements, especially of polyphagous insects, carry pests between alternative crop, pasture, weed and native host-plants (Farrow and McDonald 1988; Mueller *et al.* 1984). Displacements vary in scale from local movements between adjacent fields to long-distance migrations between different climate zones. In mixed cropping systems, local movements are sufficient for many pests to exploit sequences of short-lived habitats in crop successions (Stinner 1979).

Temperate-zone cropping regions with severe winters which pests cannot survive may be recolonised each spring by immigrants from lower latitudes (Sparks 1986). Similar movements occur in the semi-arid tropics where crop phenology varies with latitude according to the advance and retreat of monsoon or wet-season rains. Such immigrations frequently lead to significant pest outbreaks because the combination of actively growing host plants and an initial lack of natural enemies and diseases is favourable for rapid population growth. Movement plays a crucial role in the ecology of insecticide resistance, both by dispersing the resistance-conferring genes and by diluting resistant populations with immigrants from untreated crops and wild hosts (Comins 1977).

Migrant species show a range of morphological, behavioural and physiological adaptations which regulate the timing of migration and the direction and distance of movement in a way that optimises reproductive success (Gatehouse 1986). Insect migrations occur both 'within generations' (i.e. during development, and affecting the survival of the insects undertaking the movement and their ability to accumulate resources for reproduction), and 'between generations' (i.e. after accumulation of reproductive resources but before oviposition, and influencing survival of the offspring). Insects adapted to short-lived habitats (e.g. solitary locusts and some noctuid moths), where no more than one generation can normally be completed before the environment deteriorates, are *obligatory* migrants. They anticipate the expected reduction in habitat quality and emigrate even if the breeding site remains favourable at the time the adults develop. Insects inhabiting environments which are not permanent but which may remain favourable for several successive generations (e.g. aphids) are *facultative* migrants. They emigrate only in response to cues (e.g. poor vegetation quality, short daylength, or crowding) which indicate that habitat deterioration is imminent.

In many species, migration is restricted to the post-teneral, pre-reproductive period of development (Johnson 1960). Migration and reproduction appear to be co-ordinated by the neuroendocrine system, with juvenile hormone stimulating both flight and oogenesis in several species (Pener 1985; Rankin *et al.* 1986). Mobilisation of fuel for flight is under the control of the adipokinetic hormones (Goldsworthy and Wheeler 1986). Fuel is usually accumulated as fat during larval development, although some Lepidoptera require a nectar feed before initiating their migration. Some species are polymorphic with respect to wing length, and proportionately more long-winged, migratory forms are produced in response to increasing density (Farrow *et al.* 1982). The capacity for flights of long duration in some migrants shows heritable variation which appears to be under the control of a number of genes (Dingle 1986; Gatehouse 1989).

Information on migration has been obtained by a variety of means (Drake 1991; Rabb and Kennedy 1979; Riley 1989; Schaefer 1976). Mark-and-capture methods have employed internal (e.g. radioisotope) as well as external marks, and laboratory-reared as well as natural emigrant populations. Naturally occurring marks that

indicate a remote origin (e.g. pollen or traces of rare elements) have been used to identify the carriers as immigrants. Observations of migrants at times or places where they could not have been produced locally, such as on ships or in regions where the species cannot overwinter, have also been used to detect immigration. An extension of this method is the technique of 'synoptic survey', in which population densities and phenologies are monitored over a wide area and immigrations and emigrations are detected from sudden changes in numbers that cannot be accounted for by local processes. Migrants have been captured in flight in nets or suction traps carried aloft on aircraft, tethered balloons, or kites. Migration has also been observed directly, either visually, sometimes with the aid of night-vision equipment, or by a variety of remote-sensing techniques. Special-purpose radar units specifically developed for insect migration studies have proved particularly valuable because they can provide high-quality information on migratory flights at altitudes up to 2 km, where even the detection of a migration is very difficult by any other means (Fig. 3.34). Indirect methods, such as laboratory measurements of flight capacity and physiological studies of fuel accumulation and flight-muscle autolysis, provide supporting evidence for migration, as does analysis of the meteorological conditions in which a migration is believed to have occurred.

Migration, Climate and Weather

Climate and weather are the predominant environmental factors that influence migration (Drake and Farrow 1988; Pedgley 1982). The annual patterns of temperature and rainfall that characterise the regional climates of the world produce the temporal and spatial changes of habitat quality to which many long-distance migrants are adapted. On a smaller scale, the erratic rainfall of semi-arid climates produces a patchy distribution of ephemerally favourable habitats that insects migrating over shorter distances can exploit (Drake and Farrow 1985). Migration provides an alternative strategy to hardiness and diapause as a means of surviving periods of climatic inclemency; it may be particularly successful where the unfavourable conditions are especially severe, as in inland North America during winter, or unpredictable, as in both the summer- and winter-rainfall zones of inland Australia.

While migrations are made in response to climatic effects, they are controlled by the weather. By assisting or disrupting migratory flight, atmospheric phenomena influence in a variety of ways the displacements achieved and the likelihood of locating a habitat favourable for developing or breeding. Take-off may be stimulated by disturbed weather (D. P. Clark 1969; Persson 1976), and rain may trigger emergence and therefore control the timing of emigration. Low temperatures suppress the initiation of migration, reduce its duration, and limit the altitude of flight. Upcurrents carry insects, including flightless species, aloft, and the wind displaces them horizontally. Wind systems exhibiting convergence can concentrate insect populations and carry them into areas where rain is falling (Drake and Farrow 1989), a process of great potential ecological importance in semi-arid regions.

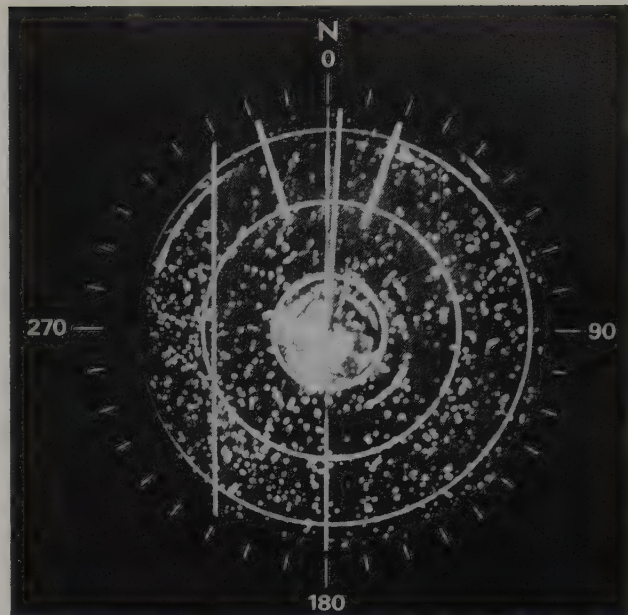


Fig. 3.34 The display of the CSIRO Entomological Radar, showing a migration of Australian plague locusts. The photograph was taken at Trangie, N.S.W. (31°59'S, 147°57'E), on 9 December 1979, at 20.45 h, with the radar beam directed upwards at an angle of 8°. The range rings represent distance intervals of about 500 m and height intervals of 65 m. Each dot on the screen indicates a single locust. It can be seen that the locusts were distributed very uniformly in space. From the number of dots and the characteristics of the radar it can be estimated that the density of locusts at heights of 100–200 m was about 10 per million cubic metres. Successive photographs taken at 3-second intervals show that these migrants were moving northwards at a speed of 12 m/s. They would have covered a distance of about 40 km since taking off at dusk about an hour earlier.

Weather has a major influence on migration partly because insects fly relatively slowly and the direction and speed of their migration is strongly influenced by the wind. Near the ground, wind speed generally increases with height. The zone in which the wind speed is less than an insect's air speed, so that the insect can fly in any direction by adjusting its heading to compensate for displacement by the wind, is known as the *flight boundary layer* (Taylor 1974). Migration within this layer allows an insect to maintain a fixed course by means of light-compass or optomotor responses (Williams 1958; Kennedy 1951). This may result in upwind movements in light winds (Mikkola 1986), and in migratory flight being inhibited when the wind is strong. Insects migrating above the flight boundary layer usually move approximately downwind, although they often adopt a common heading direction which is not fixed, but appears to be related in some way to the wind (Drake 1983; Riley and Reynolds 1986). The cues used to achieve orientation at high altitude, usually at night, have not yet been identified.

The structure and internal motions of the atmosphere in which the insects are flying determine many of the characteristics of high-altitude migrations (Drake and Farrow 1988). Because the atmosphere below about 2 km takes on quite different forms by night and by day, nocturnal

and day-time migrations have markedly different characters. The atmosphere over land is normally stable at night and for 1–2 h after dawn, so that there are no large-scale updrafts and downdrafts. Once the dusk take-off is completed, a uniform, unidirectional, approximately downwind migration usually develops. This may persist throughout the night, but there is often a progressive decline in numbers, with little activity after midnight. Migration may occur at altitudes up to 2000 m, but densities are most often greatest at heights between 100 and 400 m. The migrants frequently form layer concentrations, i.e. they collect in relatively narrow altitudinal zones, where temperature, wind speed, or wind direction are most favourable for migratory flight (Drake 1984). These concentrations often form near the top of the nocturnal temperature inversion, and are sometimes associated with a low-level jet, a zone a few hundred metres deep in which the wind is stronger than in the general airflow above and below it (Drake 1985a). Wind-assisted migrations at speeds of 10–20 m/s, lasting 3–5 h, and covering distances of 100–400 km, are common at night. Migrations that continue throughout the night often cease suddenly at dawn, but some continue into the day, especially when the migrants have flown out over the sea (Drake *et al.* 1981). Insects migrating at night include not only nocturnal species like moths and crickets but also those which are active by day, such as locusts and many Hemiptera.

Day-time migration above the flight boundary layer normally commences with the onset of convective updrafts and downdrafts which are produced by solar heating of the ground. Insects are carried into updrafts by convergent airflows at the surface. There is usually no corresponding dispersal of the migrants at the top of the updraft because the airflow becomes divergent only above the insects' flight ceilings. Day-time migrants therefore become concentrated in updrafts where they can remain aloft with less consumption of energy than would be necessary in a stable atmosphere. The convective motions tend to become organised into hexagonal cells and parallel 'streets' aligned downwind (Schaefer 1976). The updrafts and the insects concentrated in them move in the direction of the large-scale airflow, but average wind speeds are reduced and displacements are typically less than half of those achieved by nocturnal migrants in similar synoptic conditions. Daytime migration at high altitude is generally favoured by micro-insects, most notably aphids (Johnson 1969). When the wind is favourable it is also employed by migrants such as butterflies and dragonflies which follow a fixed bearing and which migrate within their flight boundary layer when there is a headwind. Micro-insects which have taken off during the day sometimes continue their migration into the night. They fly above the nocturnal temperature inversion, which sometimes begins to form before dusk, and may be inhibited from terminating their flight by the lower temperatures they encounter on beginning a descent (Farrow 1986).

Small- and medium-scale atmospheric motions can also disturb the stable night-time airflow and affect the

displacements of nocturnal migrants. Like convection, these disturbances often include regions of convergent airflows which concentrate the migrants that encounter them. Outflows of cold air from thunderstorms rapidly collect migrants into a line concentration at the flow's leading edge, and carry them for distances of 10–20 km in a direction that may be quite contrary to the general airflow (Pedgley *et al.* 1982; Schaefer 1976). Sea breezes have a similar effect but operate over a large scale (Drake 1982). They can extend far inland where they often arrive during the first half of the night when migration is at its peak. In regions of sloping terrain, downslope drainage winds may strongly influence nocturnal migrations. Insects flying at night sometimes encounter atmospheric wave motions (Drake 1985b), but these usually have only a transient effect on the migrants' trajectories.

Long-distance migration is controlled by large-scale airflows and by weather phenomena associated with major disturbances to these flows. In the tropics and subtropics, migration occurs primarily on the opposing trade-wind and monsoon airflows, and is influenced by seasonal and short-term movements of the boundary between these flows and by disturbances such as tropical troughs and cyclones. The migrants follow the changing rainfall pattern associated with the advance and retreat of the monsoon. In temperate regions, migration is usually a response to seasonal variations in temperature, with movements to higher latitudes in spring generally coinciding with the commencement of the growing season in the destination region, and sometimes also with the onset of hot-dry conditions at the source. These poleward movements occur on fast-moving flows of warm air that develop to the west of an anticyclone and immediately ahead of the following depression and cold front. Flows in other directions occur behind the front, and a particular source region will experience a sequence of wind directions as the pressure systems and fronts pass overhead, moving in the west-to-east direction characteristic of temperate-zone synoptic disturbances. Emigration flights may therefore occur in all directions, but intensities and displacements usually decrease after the front has passed, initially because the temperature is much lower and later because the wind becomes light (Drake and Farrow 1985). Temperate-zone weather therefore generally favours migration to higher latitudes, and this is true in the autumn, when it disadvantages emerging migrants, as much as in the spring, when it greatly assists them. However, in some geographical regions, most notably eastern Asia, more persistent seasonal airflows develop which tend to carry insects polewards in spring and back towards lower latitudes in autumn.

Migration in Australia

Australia extends into both the tropical and temperate zones, but most of the continent lies in the warm, semi-arid belt at the boundary of these two climate regimes. In most of the interior, vegetation growth is limited by rainfall which is often erratic and which varies considerably from season to season. In the northern tropics and subtropics, rain and vegetation growth occur mainly in

summer. Much of this rain originates in convective storms and has a very patchy distribution. In the temperate southern inland, rainfall peaks in winter or is distributed evenly through the year, but much of the summer rainfall is lost to evaporation, and plant growth occurs predominantly during the cooler months. Along much of the eastern seaboard, conditions are favourable for growth throughout the year.

These geographical and climatic factors provide many opportunities for migratory insects to exploit. In the south-east, Australian plague locusts *Chortoicetes terminifera* (Farrow 1977a), noctuid moths (Drake and Farrow 1985; Drake *et al.* 1981; Farrow and McDonald 1988), lygaeid bugs (McDonald and Farrow 1988), bush flies (Hughes and Nicholas 1974) and aphids (Johnson 1957) and a wide range of other micro-insects from over 7 orders (Farrow 1982c), develop in large numbers in inland regions during winter and move southward in spring towards the cooler tablelands and coasts of the southern periphery of the continent (Fig. 3.35). These movements are made on warm airflows ahead of cold fronts. The migrants may be carried out to sea (Farrow 1975), and sometimes reach Tas. and even New Zealand (Drake *et al.* 1981; Fox 1978; Tomlinson 1973). Most species attempt to breed on arrival in the invaded areas, but the bogong moth *Agrotis infusa*, which is univoltine, spends the summer in aestivation high in the mountains (see p. 69). This is the only migrant for which there is good evidence of a return migration from the continental periphery in autumn (Common 1954b). A southward movement of bush flies also occurs in spring in south-western Australia (Matthiessen 1983).

Within the inland, movements can occur in a variety of directions as temperatures are often above the threshold for flight even when the wind is from the south. This is especially true in the subtropics, but northward move-

ments of moths (Drake and Farrow 1985) and locusts (Drake and Farrow 1983) also occur in the temperate inland. These movements allow the migrants to locate favourable habitats within their primary range and may be more important for the long-term survival of the species than the mass migrations that carry them far to the south. Thus the Australian plague locust, for example, is probably adapted primarily for survival in south-western Qld, where it appears to be endemic. The locusts migrate within this region in order to exploit ephemeral patches of breeding habitat. In seasons with heavy summer rains, breeding is widespread and an outbreak is initiated (Wright 1987). Subsequent generations that are carried south into the temperate zone tend to become trapped there as winds sufficiently warm for migration then come mainly from the north. The outbreak ends when a generation either succumbs to hot, dry conditions over summer or migrates out to sea and perishes.

Further east in Qld, high-altitude migration is predominantly towards the west in summer, under the influence of sea breezes and the prevailing trade winds (Drake and Farrow, unpubl.). These movements enable insects from coastal regions to colonise inland habitats that become favourable during the period of summer rainfall. Temporary reversals of the prevailing airflow cause eastward movements which may lead to the migrants being carried out to sea (Farrow 1984; Fletcher 1973a).

Immigration into northern tropical Australia from the Indo-Melanesian archipelago appears to be minimal, even though winds are occasionally favourable for transporting insects across the Timor and Arafura seas during the monsoon season. This is probably due to the small size of the source areas and to the short duration of migratory flights on tropical islands (Riley *et al.* 1987). A sustained surge of the monsoon in 1973 may have provided conditions suitable for south-eastward movement across the north of Australia by a range of migratory species. This is suggested by the sudden development of resistance to DDT in the cotton bollworm *Helicoverpa armigera* in eastern Australia during that year; previously, resistance was confined to the far north of W.A.

Day-time movements in fixed directions within the flight boundary layer have also been recorded in Australia, mainly by butterflies. The caper white, *Anaphaeis java teutonia* (Pieridae), a number of other pierid species (Smithers 1983b), and the Australian painted lady *Vanessa kershawi* (Nymphalidae) (Smithers 1985), all commonly make this type of migration. The monarch or wanderer butterfly, *Danaus plexippus plexippus* (Nymphalidae), an introduced species, migrates to and from overwintering colonies in the Sydney region (James 1986), a behaviour similar to that of the species in its native North America. Low-flying swarms of Australian plague locusts move steadily towards the south-east irrespective of the wind direction (Farrow 1977a).

Several migrant species are serious pests of Australian agriculture. Australian plague locusts can cause extensive damage in south-eastern Australia, especially in the high-value, irrigated crops of the Riverina (Wright 1986b). Management of the species is co-ordinated by the

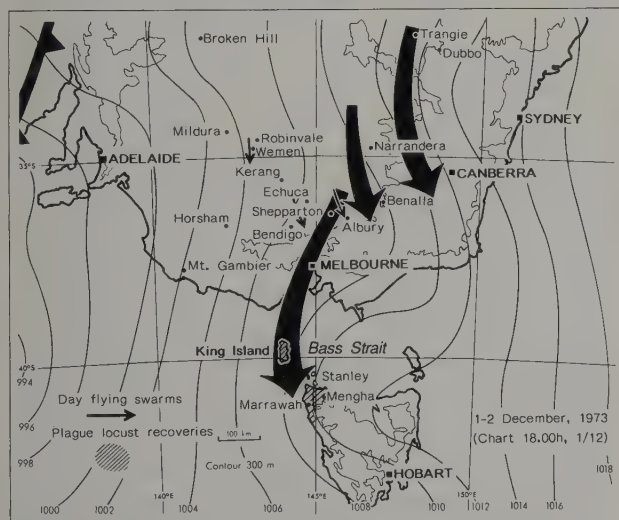


Fig. 3.35 Migrations of Australian plague locusts on 1-2 December 1973, showing southward drift of day-flying swarms and longer-distance night movements from the inland towards the continental periphery and out to sea. The migrations were in a northerly airflow ahead of a cold front, and occurred far to the south and east of the main range of the locust. Such migrations mark the final stage of a locust outbreak.

Australian Plague Locust Commission which endeavours to detect and control outbreaks during their early stages in the pasturelands of western Qld and N.S.W. so that migration into areas of more intensive agriculture is prevented (Wright 1987). Infestations of Rutherglen bug, *Nysius vinitor* (HEMI: Lygaeidae), the major pest of sunflowers throughout eastern Australia, are commonly initiated by immigration in spring and summer (McDonald and Smith 1988); the species is found far into the inland and intense southward migrations have been detected in central western N.S.W. (McDonald and Farrow 1988). The aphids *Acyrtosiphon kondoi* and *Therioaphis trifolii* f. *maculata*, introduced into Australia in 1977, have spread rapidly by migration and invaded all the lucerne-growing areas of south-eastern Australia. The biting midge *Culicoides brevitarsis*, the vector of Akabane virus, which causes calving losses in cattle, is occasionally carried into the tablelands of N.S.W. from overwintering regions in the Hunter Valley and along the north coast by easterly winds; these infrequent movements lead to epizootics of the disease, because pregnant cows in the invaded areas have not usually been infected previously and are therefore all susceptible. The common armyworm, *Mythimna convecta* (LEPI: Noctuidae), an important pest of barley throughout the cereal-growing belt of southern Qld, N.S.W. and Vic., migrates southwards in spring to infest young crops early in the growing season (Farrow and McDonald 1988; Smith and McDonald 1986). Similar

migrations are made by various cutworms (*Agrotis* spp.) and sometimes also by the southern armyworm, *Persectania ewingii*, (Drake *et al.* 1981; Drake and Farrow 1985); these species occasionally cause minor damage to crops as far south as Tas. The native budworm, *Helicoverpa punctigera*, migrates into intensive irrigated cropping areas in central and northern N.S.W. and southern Qld in spring (Farrow and Daly 1987), and is a major early-season pest of cotton; the moths probably originate in native vegetation and pastures to the north and west. These pests are all native insects that are adapted primarily to the ephemeral vegetation of inland Australia but are capable of exploiting the patchy and short-lived habitats of arable cropping systems when these contain suitable hosts. The cotton bollworm, *Helicoverpa armigera*, the most important pest of cotton in Australia, is less migratory than *H. punctigera* and is largely confined to cropping areas; this may account for its development of resistance to both DDT and pyrethroid insecticides. Populations in different parts of eastern Australia cannot be distinguished by electrophoresis, however, which suggests that some mixing over long distances occurs (Daly and Gregg 1985). This species may therefore be a facultative migrant; it is polyphagous, and may be able to survive almost continuously within a cropping area by making short-distance movements between alternative crop hosts, and, in temperate regions, by spending the winter in pupal diapause.

Principles and Practice of Systematics

P. S. CRANSTON, P. J. GULLAN *and* R. W. TAYLOR

The authors of the various chapters of this book are predominantly entomological taxonomists or systematists. These are scientists who study various aspects of the description, naming, classification, identification, phylogeny and biogeography of insects. In this chapter, *taxonomy*, the theory and practice of describing, naming and classifying is distinguished from *systematics*, the scientific study of the diversity of and relationships between the different organisms. Elsewhere the terms sometimes are used interchangeably.

Many entomological taxonomists, perhaps overwhelmed by documenting the astonishing numbers of species of insects, only describe groups (*taxa*). Others, systematists, consider *phylogenetics*, the elucidation of patterns of relationships and interpretation of their origins, to be the major motivation in their research. Of course, there is a continuum of study from the purely descriptive to investigations of phylogeny and related matters such as historical biogeography (Chapter 8).

Classification is the division of objects into classes. Objects within a class either more closely resemble each other than they do excluded objects or are more closely related to each another than to any excluded object. Resemblance and relatedness may be the same but are not necessarily so. Classification is not restricted to biology, since inanimate objects may be classified. Entomological taxonomists classify the Insecta—other taxonomists study different groups of fauna and flora, both extinct (palaeotaxonomy) and extant. *Identification* is not synonymous with classification, since identification takes place within a pre-existing classificatory framework.

Classifications are hierarchical arrangements of groups

within groups, representing different degrees of inclusiveness. In biological classifications the levels (categories or ranks) represented in this hierarchy bear names, the application of which are governed by rules of *nomenclature* (see pp. 121–2). The most fundamental nomenclatural category is the species which is placed into increasingly inclusive categories, both obligatory and optional. Those categories most widely used in entomological nomenclature are given in Table 4.1, with their standard suffixes; obligatory categories are shown in capitals (see p. 121).

One important function of the biological classification system is that it provides for an information storage and retrieval system of great capacity. A name that identifies a species provides a label for the totality of biological knowledge pertaining to that animal. For example, knowledge that an insect belongs to the order Diptera informs us that it is a true fly, possessing only one pair of mem-

Table 4.1 Taxonomic categories

Taxonomic Category	Standard Suffix
ORDER	
Suborder	
Superfamily	-oidea
FAMILY	-idae
Subfamily	-inae
Supertribe	-itae
Tribe	-ini
Subtribe	-ina or -iti
GENUS	
Subgenus	
SPECIES	
Subspecies	

branous wings, with the metathoracic wings forming halteres. The further information that this dipteran belongs to the family Calliphoridae leads to recognition that this is a 'blowfly' or 'bluebottle', characterised by a particular suite of morphological characters and by behaviours that include carrion feeding by the larvae (maggots). Identification of this calliphorid as belonging to the genus *Lucilia* tells us that this belongs to a group of metallic-coloured blowflies with larval biologies that include induction of myiasis in humans and animals. Final identification that the calliphorid belongs to a species called *Lucilia cuprina* reveals that this is the 'green sheep blowfly' that causes most primary fly strike to sheep in Australia. These names of taxa of various ranks, but particularly that of the species, allow access to the voluminous literature on the physiology, biochemistry, ecology, behaviour and agricultural economics of this pestilential fly.

The second major function of classifications is to allow biological prediction. Entomologists, faced with a plethora of little known, undescribed or newly described taxa, largely lack adequate species-level data. Classifications have a powerful heuristic function, allowing integration and extrapolation of knowledge from well known species to make predictions about their lesser known relatives.

Classifications differ in their abilities to make sensible predictions. 'Special' classifications, for example based upon geographic distribution, pest status, or a single life history stage, are limited in their ability to predict other features. In contrast, 'natural' classifications have greater predictive value. Discussions on the meaning of 'naturalness' in classifications continue (e.g. Gilmour 1940; Sneath and Sokal 1973; Farris 1979a; Platnick 1979; Patterson 1982). Briefly, two interpretations exist: that a 'natural' classification reflects evolutionary history, or 'naturalness' reflects the pattern of nature without recourse to speculations on process. Optimal classifications should have maximum predictivity for new characters and/or new taxa (Farris 1979b; Archie 1984).

Systematists use various methods to deduce pattern and relationships. The incorporation of new or different data and/or the use of different analytical approaches may have a significant effect upon classification. Thus the classifications used in this book may be contrasted with those of the 1st edition (CSIRO 1970). Changes have been made, some of which are quite major. Even within this book, the higher level phylogeny (and hence classification) proposed by Kristensen (Chapter 5) differs from that of Kukalová-Peck (Chapter 6) although both avowedly use a similar (cladistic) method. Such dissenting views arise because different systematists may base their analyses on different data (see p. 113), or may analyse and/or interpret data differently (see p. 114). Taxonomic judgment, based on familiarity with the biology and characters of the insects, is an integral part of classification.

In this chapter we endeavour to explain how taxonomy is done and demonstrate differing views on the nature of the relationship between theories of pattern and phylogeny and hence of classification. More extensive coverage of descriptive taxonomy can be found in Blackwelder

(1967), Mayr (1969) and Abbott *et al.* (1985) and more detailed (and discordant) views on phylogenetics may be obtained from Sneath and Sokal (1973), Eldredge and Cracraft (1980), Wiley (1981), Ridley (1986), Hawksworth (1988) and Levinton (1988).

THE TAXONOMIC PROCESS

Choice of Study Group

Boundaries of a taxonomic revision must be defined since time, financial constraints and user requirements effectively prevent open-ended studies for all but a wealthy amateur. Increasingly, studies involve groups of perceived applied importance, where economic significance (agricultural, biocontrol, medical or veterinary) is emphasised, to the neglect of other taxa. Some groups appear more promising than others in resolving problems of biogeography, ecology or evolutionary theory. Aesthetics may direct attention: butterflies are better studied than microlepidoptera. Furthermore, taxonomists often follow their mentors or predecessors, revising groups with pre-existing but outdated taxonomy, rather than commencing study of novel groups that lack an established framework.

The uneven distribution of Australian expertise and the concentration of taxonomic effort into the better known sections is documented by Richardson (1984). The Australian Biological Resources Study (ABRS) seeks to rectify this imbalance and to broaden the scope of Australian taxonomy through the identification of neglected groups and sponsorship of their study (Richardson 1987; Anon. 1988b).

The Australian insect fauna remains poorly known, with R. W. Taylor (1979) estimating that less than half the species were described. However, recent studies in tropical ecosystems have greatly increased our estimates of insect diversity (Erwin 1982; May 1986; Janzen 1987; Stork 1988), which previously were based on temperate faunas. Therefore, current Australian estimates are likely to be very conservative (New 1984c). Thus the lack of adequate taxonomic knowledge that Taylor (1976, 1983) identified as the *taxonomic impediment*, the barrier to recognition and naming of taxa in, for example, environmental and ecological programmes, is of even greater magnitude than previously recognised. Increasing awareness of the importance of invertebrate conservation (e.g. Collins and Wells 1987; J. D. Majer 1987; Hill and Michaelis 1988) highlights the need for greater taxonomic knowledge of our fauna, but is as yet unmatched by increased resources (Wilson 1985c; May and Seger 1986).

Geographic Scope

After selection of a study group, the geographic scope must be considered. Ideally, revisionary taxonomic studies should be world-wide, allowing incorporation of all available biological data and recognition of biogeographic patterns. However, studies typically are constrained geographically, for example, to continental Australia or a specified biogeographic sub-unit. Even in such con-

strained investigations, extralimital information cannot be ignored, either for nomenclatural, biogeographic or ecological reasons. For example, many economically important species have been distributed by human agency across biogeographic boundaries. Thus even applied studies must be sufficiently broad to allow pest species to be placed into the broad evolutionary, biogeographic and ecological perspective.

Collection and Preservation

Most taxonomic studies are based initially upon examination of pre-existing material, but additional specimens later may be acquired to help resolve outstanding questions on species diversity, morphological variation and geographic distribution. These additional specimens may also provide additional biological information such as host specificity and phenology. Such information may require specialist rather than general collecting techniques. Methods for collection of insects from natural habitats, their *curation* (preparation, maintenance and preservation) and their study in collections, vary greatly depending on the taxon, the life history stages involved and their biology.

Traditional collecting and curatorial techniques are well explained by J. E. H. Martin (1977), Dahms *et al.* (1979), Upton (1991) and Smithers (1981). Recent recognition of the high diversity of canopy insects has stemmed from the use of novel sampling techniques. These techniques include canopy fogging, which is the use of pyrethroids to knock down arboreal arthropods (Roberts 1974; Erwin 1983), and the adoption of equipment such as cherry pickers, canopy towers, walkways and ropes (Perry 1978; Landsberg and Gillieson 1982; Sutton 1983). The ecological requirements for quantified sampling and subsequent analysis of entomological data are covered for terrestrial insects by Southwood (1978) and for aquatic, benthic invertebrates by Elliott (1977).

The collecting of insects requires attention to conservation values and permits are required in national parks, reserves and state forests. Information on Australian collecting permits can be obtained from the appropriate state or territory authorities, details of which are summarised in Anon. (1986). Increasingly countries protect their flora and fauna by national and international agreements. Monteith (1987) details Australian legislation on import/export controls.

Taxonomic Collections

Insect specimens collected for taxonomic purposes are valuable only if they are available to the wider scientific community. Reference specimens from ecological, physiological, genetic and biocontrol studies, termed *voucher specimens*, are equally important. All specimens should be clearly, unambiguously and informatively labelled, with the minimum information being: place of collection (preferably including map coordinates), date and name of collector. Additional information can include habitat, behavioural details, host information and collection method. Reliance on cross reference from specimen to field notebook should be restricted to non-essential data.

Material should be entrusted to a museum or similar institution where it will be preserved and accessible for research purposes. The depository of taxonomic and voucher specimens should be specified in publications. Generally, material should be deposited in an appropriate national institution. Collecting permits often specify the depository for authorised specimen collections. Where material resides in a personal or non-taxonomic institutional collection there may be problems of subsequent availability if the long-term fate of the collection is uncertain. Arnett and Samuelson (1986) give a comprehensive list of the repositories of the world's insect and spider collections.

The existence of established collections means that taxonomy is a science with a large historical component. Taxonomic revisions must consider all relevant material studied by previous workers because the *International Code of Zoological Nomenclature* demands that the oldest available valid names be applied (see 'Principle of Priority', p. 122). Furthermore, earlier collections contain much valuable information and allow a more comprehensive treatment.

The historical materials required for taxonomic revision often reside outside the country of collection. For example, most early descriptions of the Australian biota were undertaken by non-Australians and many important collections remain outside the country (Chapter 8, see also R. W. Taylor 1983). Material may be in obscure institutions and, although maintenance is a scientific duty, the passage of time and waning of enthusiasm for collection maintenance may make the tracing of material a laborious, if not impossible, procedure. Nevertheless, the taxonomist must expect to visit, or at least liaise with, curators of international collections.

The nature of these problems may be demonstrated by Houston and Watson's (1988) documentation of the four dragonfly species of the cosmopolitan coenagrionid *Pseudagrion* in Australia. The five names (one a synonym) were proposed individually between 1842 and 1926 by three authors in four different journals in three languages. Information on the subsequent taxonomy, distribution and biology may be found in a further ten publications. The specimens upon which the species descriptions were based are held in four institutions, three of which are non-Australian and the type material of one name is believed to be lost.

Taxonomic Literature

Many insect groups are encumbered with species descriptions that are inadequate by modern standards. Descriptions may be scattered through more than two centuries of taxonomic publications in a wide variety of languages (as exemplified in *Pseudagrion* above). Thus, taxonomy necessitates access to extensive libraries containing important, if infrequently consulted, journals and books. The taxonomist must be cognisant of all predecessors' published views, especially concerning the legal regulations and recommendations of the *International Code of Zoological Nomenclature* (see pp. 121–3). Compendious works, such as *The Insects of Australia*,

can only serve as an entry point to the vast taxonomic literature.

Catalogues or checklists are valuable sources of taxonomic information, usually covering circumscribed groups and regions (Thompson and Knutson 1987). The minimum information contained in such works is an ordered list of described taxa. Further data, such as geographical distribution, specimen repositories, nomenclatural histories and bibliographies are recorded in increasingly extensive catalogues. For some taxa comprehensive bibliographies are available. Compilation of catalogues and bibliographies, although time-consuming, is a vital exercise in taxonomic and nomenclatural 'house-keeping' and an essential precursor to taxonomic studies. Taxonomists often maintain card indexes, but these are of limited availability and cross referencing is restricted. Published catalogues become dated as subsequent studies lead to additional descriptions and revised opinions. With the advent of computers, electronic databases are increasingly produced (Thompson and Knutson 1987). The Australian Biological Resources Study recognises the importance of publishing catalogues of the described Australian fauna (e.g. Houston 1988) as well as producing and updating them in electronic form. These serve as an aid to users of taxonomic information and to the taxonomic community itself (Anon. 1988b).

The Species

Some taxonomic studies deal only with *higher classification* (above species level), with the systematist accepting the inclusive groupings obtained by previous authorities. These studies have a vital role to play in systematics. The classifications below ordinal level and the chapter sequence used in this book integrate many such synthetic studies. Predominantly however, formation of species groups, subgenera, genera and still higher groupings result from studies that commence at the species level.

The term species is difficult to define because it is used for a taxonomic category, a biological concept and a unit of evolution. Definitions of species differ in their emphasis of actual and potential reproductive isolation (the *biological species concept*; Mayr 1942, 1982), independent history (Simpson 1961; Wiley 1978) and behaviour (e.g. specific mate-recognition systems; Paterson 1980, 1985). Biological species concepts are widely (e.g. Coyne *et al.* 1988) but not universally (e.g. Loevtrup 1987) accepted, but direct evidence of reproductive isolation is rare. Nevertheless, *taxonomic species* or 'morphospecies' (recognised on morphological grounds) often, but not always, appear equivalent to biological species (Futuyma 1986).

Some systematists have emphasised the relative importance of different modes of speciation, particularly in insects (e.g. Bush 1975; M. J. D. White 1978; Butlin 1987). The prevalent mode which is assumed in the absence of contradictory evidence is *allopatric speciation*, that is differentiation following (i) segregation of a formerly widespread population into two or more isolates by the formation of a geological or ecological isolating barrier (a *vicariance event*) or (ii) dispersal across a pre-

existing barrier by a small (*founder*) population (Cracraft 1984). Speciation in the absence of geographical barriers can be *sympatric* (in the same geographical area) or *parapatric* (in contiguous, but non-overlapping areas). Speciation modes cannot readily be identified by current distribution, since range changes can lead to secondary contact and overlap. Further discussion of this topic is beyond the scope of this book but readers may refer to reviews such as Futuyma (1986), Coyne and Orr (1989) and Otte and Endler (1989).

In practice, for many biparental and all asexually reproducing taxa, only morphological criteria are readily accessible for species recognition. Predominantly this relies upon detection of one or more morphological discontinuities among otherwise similar organisms. A spectrum of ease of differentiation exists, running from one or few unique attributes to overlapping ranges of features, none of which individually characterise the taxon. In some instances discussed below, anatomical details may be insufficient to identify species recognised on other grounds. Furthermore, the discovery of morphological discontinuities that delimit species in one life history stage does not necessarily indicate that other stages can be discriminated.

The existence of morphologically similar or identical populations for which there is evidence or inference of reproductive isolation is a problem. Recognition of such pairs or groups (*complexes*) of species, termed *sibling species*, is of practical importance, particularly in applied fields, and of theoretical significance in relation to the speciation process. The detection of sibling species most often arises from non-morphological evidence, such as differential vector capacity, host specificity, phenology or mating behaviour. Re-evaluation of morphology may subsequently allow species segregation.

The presence of giant polytene chromosomes in many medically important Diptera has allowed detection of karyotypic segregates. Australasian sibling species have been identified, for example, in the blackfly (DIPT: Simuliidae) genus *Simulium* (Bedo 1977) and the mosquito (DIPT: Culicidae) '*Anopheles farauti*' (Mahon 1983). In the latter case, chromosome banding patterns confirmed sibling species recognised through hybrid sterility. Although sibling species of *Anopheles* and *Simulium* differ in their ability to transmit human disease in other countries (G.B. White 1974, 1978; Shelley *et al.* 1987), comparable differences in biology and vector status of the Australian species are unknown.

The consequences of failure to recognise sibling species can be costly. The prickly pear (*Opuntia* species) outbreak described by Waterhouse (Chapter 7) was not controlled immediately by introduced *Cactoblastis* species. Although early and some subsequent failures have been attributed to unsuitable climate, this appears unlikely in view of the recognised existence of sibling species that vary in their host specificity (McFadyen 1985). Morphologically similar species complexes with specific host associations have profound implications for biological control programmes (McFadyen 1985; Cox 1983). The detection of sibling species in *Cyrtobagous*

weevils intended for biocontrol of *Salvinia* (Sands 1983) exemplifies the phenomenon of polyphagous 'species' being found to be complexes of narrowly oligophagous or monophagous species.

Human head and body lice (*Pediculus capitis* and *P. humanus*) are examples of sibling species in which proven reproductive isolation is reflected by only slight morphological differences previously believed to represent polymorphism related to segregation on the host (Busvine 1978). Behavioural indications of the existence of sibling species may include song, particularly in Orthoptera. For example, in *Metaballus* katydids (ORTH: Tettigoniidae), Rentz (1985) found male songs distinguished species possessing only subtle morphological differences, previously ascribed to individual variation.

Variability of Species

Phenotypic variation, resulting from genetic or environmental influences, complicates the delineation of species. Genotypic variation may be manifest in many polymorphisms (see Chapter 3, and Vane-Wright and Ackery (1984) on butterflies) and sexual dimorphism in which secondary sexual characters differ between males and females (e.g. Cook 1987). Predominantly environmental effects include phase polymorphisms (Chapter 3), caste polymorphisms (termites, Chapter 20; ants, Chapter 42) and the ecophenotypic components of geographic variability.

The effects of host on insect phenotype may be dramatic. In species of armoured scales (HEMI: Diaspididae), leaf and stem dimorphism can be so great that morphs were sometimes considered to be generically distinct (Knipscher *et al.* 1976). In dimorphic caterpillars of the geometrid *Nemoria arizonaria*, mimicry modelled on oak catkin or twig is mediated by dietary tannins (Greene 1989).

Polytypic species are those that may be divided into two or more geographic races that may be termed *subspecies*. However, Wilson and Brown's (1953) suggestion that the term *subspecies* be abandoned is increasingly accepted (Futuyma 1986). Many former 'subspecies' have been shown ultimately to be 'good' species and many putative geographic races have proved to be artefacts of insufficiently representative collections. For example, the Australian field crickets *Teleogryllus commodus* and *T. oceanicus* (ORTH: Gryllidae) were originally regarded as geographic races, but identification of reproductive isolation, by male song, was followed by the discovery of extensive sympatry without hybridisation (Hill *et al.* 1972). Nonetheless, cases are known of morphologically distinct but only partially intersterile 'races' for which the term subspecies may be retained.

Examples of geographic variation that lead to problems in species recognition include complete geographic isolation (*disjunction*) with variable degrees of differentiation and the existence of *clines* or character gradients in contiguous populations (see Endler 1977). Clinal variation may be such that populations at the extremes of the range may be distinct enough in morphology to be recognised as separate species, although intervening populations

intergrade. Clines in different features may be concordant and correlated with geography, or may be discordant. Knowledge of geographic variation can have practical importance in, for example, biological control programmes that depend upon recognition of physiological intraspecific variants (*biotypes*) of target and potential control agents (Sands and Harley 1980; Chapter 9).

Intraspecific *allometry*, differential growth of body parts (Gould 1966), can complicate species discrimination. Allometry can occur in the relationship between: (i) the same structure in different sized individuals of one stage, (ii) identical structures in consecutive developmental stages, or (iii) different structures in the same or consecutive stages. Thus, although Dyar's 'law' suggests that there is a relatively constant geometric progression in size of sclerotised structures at each moult (Chapter 2) deviations do occur (Brown and Davies 1972). Where present they invalidate extrapolation of 'diagnostic' characters such as ratios and shapes from one instar to another.

Analysis of variation involves *morphometrics*, the measurement of the morphology of geographically, ecologically and statistically representative samples and their appropriate mathematical treatment. Cook's (1987) study of sexual dimorphism and allometry in two species of dung beetles (Scarabaeidae) is an excellent example of the use of one multivariate morphological approach. The diversity of multivariate analyses available are treated extensively in Pimentel (1979) and reviewed with reference to insect studies by Daly (1985). The heuristic value of such analyses is influenced by subjectivity inherent in character selection and coding.

Characters and Character States

The use of the term 'character' is often inconsistent. A *character* (e.g. 'eye colour') is an observable feature of a taxon that is variably exhibited in subdivisions called *character states* (e.g. 'red, blue, yellow'). An *attribute* is the possession or exhibition of a particular state of a character (e.g. 'has red eyes'), mistakenly called a character state by many authors. In the sense used here, a character consists of a group of mutually exclusive attributes that are alternative expressions of the same thing (i.e. are homologous, see below) (Colless 1967; Platnick 1979; Watrous and Wheeler 1981). Ecological and distribution data are not characters in this sense. Their *a priori* use in species discrimination is to be avoided, but they can provide evidence of taxonomic status and should be recorded.

The characters used by taxonomists may refer to any item of information about a species in any phase of development, from egg or sperm, through larval or nymphal stages to the adult. Characters derived from the immature stages of some groups of insects have long been applied in species recognition, in elucidation of phylogeny and in classification (e.g. Thienemann 1908; Edwards 1926) and their significance is increasingly recognised in many others (e.g. Miller and Kosztarab 1979; I. J. Kitching 1984a; Goulet 1979). In any stage, all aspects of external and internal anatomy, colour, physiology, cytology, genetics, biochemistry and behaviour may be of value.

Traditional discriminatory characters were predominantly easily visible and external but did not always adequately segregate species. The extraordinarily diverse external and internal terminalia (Chapter 1) often give useful characters. Sometimes characters may be difficult to evaluate even with the light microscope and here the advent of electron microscopy has provided a dual function in interpretation and illustration of ultrastructure (e.g. Taylor and Beaton 1970).

Behaviour, especially that associated with mating, such as song and dance, has proved fruitful in insect taxonomy (e.g. R. D. Alexander 1962). Other non-morphological characters, including chemotaxonomic (e.g. pigments, Banks 1977; pheromones, Horak *et al.* 1988), chromosomal (e.g. Martin 1979; John *et al.* 1987), immunological, electrophoretic (Richardson *et al.*, 1986) and molecular (DNA/RNA sequence, e.g. Field *et al.* 1988; Simon 1988) data, are valuable, particularly in recognition of sibling species. Increasingly these techniques are helping to elucidate relationships (Baverstock 1987) and date origins and determine colonisation sequences of taxa, for example, Hawaiian drosophilid flies (Beverley and Wilson 1985; Carson 1987). However, despite these techniques, morphology still provides the principal means of recognition of taxa.

Most taxonomic species are recognised by a small set of *diagnostic* or 'key' character states that unambiguously differentiate that taxon from any other. Selection of diagnostic characters involves comparing and contrasting character states between taxa and distinguishing homology from homoplasy.

Homology and Homoplasy

Homology is the most important principle in comparative biology and is central to any discussion of phylogenetic reconstruction (Bock 1974; Patterson 1982). To be comparable and informative, characters must be *homologous*. Classical definitions of homology concerned identity or 'sameness', which was recognised as being due to common ancestry subsequent to the work of Darwin (1859). Different definitions of homology were reviewed by Patterson (1982), who recognised that homology could be tested by: (i) conjunction (homologous character states cannot occur in the same organism), (ii) similarity in topology, ontogeny and composition, and (iii) congruence with other homologies. Although philosophical schools differ, homology can be defined as pertaining to an ancestral relationship between features (in two or more organisms) that have evolved from the same feature in the most recent common ancestor of these organisms (Holmes 1980). Thus, the mesothoracic wings of adult Diptera and male coccoids are homologous as wings, being uniquely derived from a common ancestor (see Chapter 5). However, diptery is not homologous in these two groups since reduction of the metathoracic pair of wings to dipteran halteres or coccoid hamulohalteres occurred independently and the functions are not even analogous (Afifi 1968). These decisions concerning homology are based on other clear evidence that, at the ordinal level,

coccoids are unrelated to the Diptera. Thus homology statements are always relative to the hierarchical level.

Seemingly identical structures that are not homologous may be *parallelisms* or *convergences*, relative terms that also relate to ancestry. Parallelism may be defined as 'the separate development of similar characters [= attributes] in two or more relatively closely related lineages on the basis of genotypic similarity inherited from a common ancestor' (Holmes 1980: 49). A particular form of parallelism, *reversal*, occurs when an acquired character state reverts to an ancestral condition. Convergence is 'the independent development of similar characters [= attributes] in two or more lineages that is not based on inherited genotypic similarity' (Holmes 1980: 49). Characters evolved in parallel thus are practically identical, while those that arise convergently may be recognised as being different by re-examination. Both these non-homologous similarities may be subsumed under the term *homoplasy* (adjective *homoplasious*). Although the term *analogy* may be used of a convergent character, it is widely used only when comparing multi-character organ systems or whole organisms in a functional sense.

PHYLOGENETICS AND CLASSIFICATION

Recognition of species, assessment of character state distributions and key construction are tasks common to all taxonomists. However, differences exist in the philosophy and method of phylogenetic reconstruction and the principles (or even desirability) of representing the results in classifications.

Classifications long predate scientific ideas on their origins. For example, 'beetle' and 'chafer' are English vernacular derivatives of the Old English word 'bitula' and the subordinate term 'caefor' (Webster 1971). Berlin (1973) reviews folk taxonomies and Waterhouse (Chapter 9) records some of the extensive faunal knowledge of aboriginal Australians. Early classifications were not theory-free, but included the search for 'natural' groupings as early as Aristotle (384–322 BC; Mayr 1969). With the advent of the nomenclatural system of Linnaeus (1707–78; Mayr 1969) and acceptance of a uniform system in place of vernacular names, interest in classification revived. The search for 'natural' groups continued, with the rejection of those based on analogy and the recognition of the importance of homology, terms formalised by Owen (1842) and defined above. Thus, elucidation of a natural hierarchy of taxa was well under way when Darwin (1859) provided a theory to explain the pattern. Darwin understood that the natural system and 'true' classification should be based on *genealogy*, that is, relationship by descent. Nevertheless, taxonomic practice changed little, for patterns of nature are detectable whether or not one understands process (Patterson 1981a). However, explanatory power had become available through evolutionary scenarios.

By the middle of the 20th century systematic methods were a heterogeneous assemblage, characterised predominantly by the intuitive recognition of the course of evolution by 'experts' in their particular fields. The evo-

lutionary transformations of a few 'important' characters were sometimes traced but there was a general failure to document all character states observed, and little discussion of homoplasy. The justification for characters used ranged from evolutionary conservativeness to postulated adaptive significance. Extant and fossil taxa sometimes were recognised inappropriately as actual ancestors. The resultant classifications were often similar to current ones, but the methods were essentially untestable and unrepeatable. This assemblage of methods, called the *narrative* (Humphries and Richardson 1980) or *traditional method* (Mayr 1981), led phylogenetics into disrepute (Patterson 1987a). By the 1950s dissatisfaction had led to the development of two contrasting approaches that were explicit in their methods. These approaches, which developed into the schools of *phenetics* (numerical taxonomy) and *cladistics* (phylogenetic systematics), forced a more explicit defence of the traditional eclecticism, which became known as *evolutionary systematics*.

Phenetics

Some systematists, responding to what they perceived as the prevalent subjectivity of the narrative approach, identified *overall similarity* (*phenetics*) as a potentially objective basis for grouping and hence classification. The term *numerical taxonomy* has been applied to this school, but as Mayr (1965) stressed, numerical methods are pertinent to all classificatory schools. Justification for a phenetic method is that natural patterns based on resemblance can be detected, whereas the pathways of the evolutionary process are unknowable.

The pioneers in the field of phenetics (Sokal and Sneath 1963; Sokal 1966; Sneath and Sokal 1973) identified the following principles: (i) the more characters used the more informative and, up to a point, the better the resulting classification, (ii) *a priori* every character is of equal weight, (iii) overall similarity between two comparable taxa is an additive function of the similarities in individual characters, (iv) degrees of similarity are non-uniform thereby allowing recognition of distinct clusters, (v) taxonomy should be empirical, and (vi) classification should be based on phenetic resemblance. Furthermore, Colless (1970b) contended that overall similarity is an estimate of phylogenetic *distance* or relationship. The demand for handling many characters could not be met until the advent of electronic digital computers. Phenetic techniques, summarised below, are more fully explained in Sneath and Sokal (1973), Goto (1982) and Abbott *et al.* (1985).

Estimating similarity—or more usually difference (taxonomic distance)—first involves selection of the objects of study (organisms, populations, species or higher taxa) called *operational taxonomic units* (OTUs). This is followed by selection of characters, recognition of their included states, recording of all attributes for all OTUs, and compilation of a *data matrix*. Each character may be *binary*, that is existing in only two discrete states, scored as 0 or 1 and coded as 0 or 1 (or A/B) in a data matrix. However, many characters are not so conveniently partitioned, exhibiting either multiple discrete states (*multi-*

state characters) or being *continuous*. A multistate character that has states that fall in some natural, acceptable sequence is *ordered*. Computer programs require character states to be coded as simple integers or measured quantities. Ordered multistate and continuous characters must be recoded (by range coding or standardisation) to a uniform scale in order to restore equal weighting across the data. A few programs necessitate multistate characters being transformed first into binary coding by methods such as additive binary coding (Sneath and Sokal 1973). Several methods have been developed to code continuous data into multistate or binary variables, as reviewed by Thorpe (1984) and Archie (1985). Archie's proposed technique, 'generalised gap-coding', as modified by Goldman (1988), appears to have general applicability. After compilation of the data matrix, *distance* (or *similarity*) *coefficients* are usually estimated between each OTU and every other, based upon all characters. There are many measures of dissimilarity/similarity available for calculation of coefficients (see Sneath and Sokal 1973). The calculated values are then tabulated into a *distance* (*similarity* or *resemblance*) *matrix* of each OTU against every other.

Two principal types of analysis, clustering and ordination, can be applied to the data or distance matrix. *Clustering* methods sort and/or group OTUs such that those within a group resemble more closely others within the group than those outside. They differ principally in the criterion for calculating distances between groups of OTU's. Clustering methods are either agglomerative (sequentially adding OTUs) or divisive (sequentially separating subsets) and yield a *phenogram* (Fig. 4.1), a hierarchical branching diagram showing degrees of similarity. The 'strength' of the clustering technique may affect the shape of the phenogram: 'weak' methods yield a more pectinate shape, 'strong' methods may give a more symmetrical one (Williams *et al.* 1971). The taxonomist must choose appropriately.

Ordination methods involve graphical representation of the distance between OTUs in a multidimensional space. No more than three dimensions can be visualised at once,

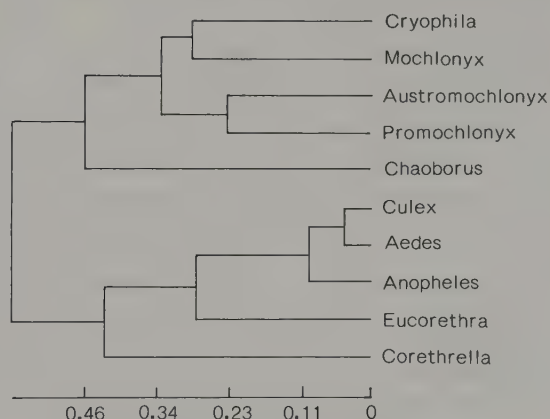


Fig. 4.1 A phenogram derived using the weighted pair-group method using arithmetic averages (WPGMA) for seven genera of Chaoboridae and three of Culicidae (*Aedes*, *Anopheles*, *Culex*)(DIPT).

[Modified after Colless 1986: Fig. 79]

but replacement of correlated characters with uncorrelated ones allows depiction of relationships in only two or three dimensions with minimum loss of 'information' (variability). Two major families of ordination methods are commonly used: (i) *principal component analysis*, using raw or normalised data and (ii) *principal coordinates analysis*, using a distance matrix. A related method *canonical variates analysis* provides the best discrimination of pre-existing groupings, particularly of geographic populations. The above methods rely on an assumption of a linear relationship between the variables and the ordination space. Another family of ordination techniques is *multi-dimensional scaling* (Kruskal and Wish 1978). One method, *non-metric multi-dimensional scaling*, permits more general, non-linear, relationships between the variables and the ordination space. Faith (1989) demonstrates the advantages of the application of this method to taxonomic data. The results of all of these analyses can be plotted in a *scatter diagram* (Fig. 4.2) usually with two, and with a maximum of three (Fig. 4.3), axes of variation represented simultaneously.

With both a phenogram and a scatter diagram, the interpretation and translation into a classification must be dealt with by the taxonomist (see p. 119).

Cladistics

Cladistics, originally termed *phylogenetic systematics*, developed from principles enunciated by the German entomologist Willi Hennig, originally in the German language (Hennig 1950) and later popularised when revised and translated into English (Hennig 1966). Concern with apparent subjectivity and consequent instability of classification led Hennig and fellow cladists such as Brundin (1966) to argue that relationship could be clearly defined only in terms of recency of common ancestry (genealogy).

In contrast to pheneticists, cladists believe that their procedures should detect genealogy. Primary among these procedures is the elucidation of *apomorphies*, derived homologous character states, which, when shared between taxa, are termed *synapomorphies*. Synapomorphic character states indicate shared (common) ancestry. Advanced character states restricted to a single taxon, *autapomorphies*, do not convey information on the relationships of that taxon to any other. Primitive states, termed *plesiomorphies*, and *symplesiomorphies* when shared, cannot indicate relationship. In Figure 4.4, the ancestral state of each character is represented by a lower case letter with the corresponding (homologous) derived condition represented by the same letter in upper case. Clearly all these terms are relative: an autapomorphy at the generic level is a synapomorphy at the species level; a plesiomorphy at the generic level is an apomorphy at some higher level.

It follows from this fundamental distinction between derived and ancestral character states that nested sets of synapomorphies of greater or lesser generality are reflections of nature's hierarchy. Every taxon of whatever rank uniquely possesses a *sister group*—a taxon which is its

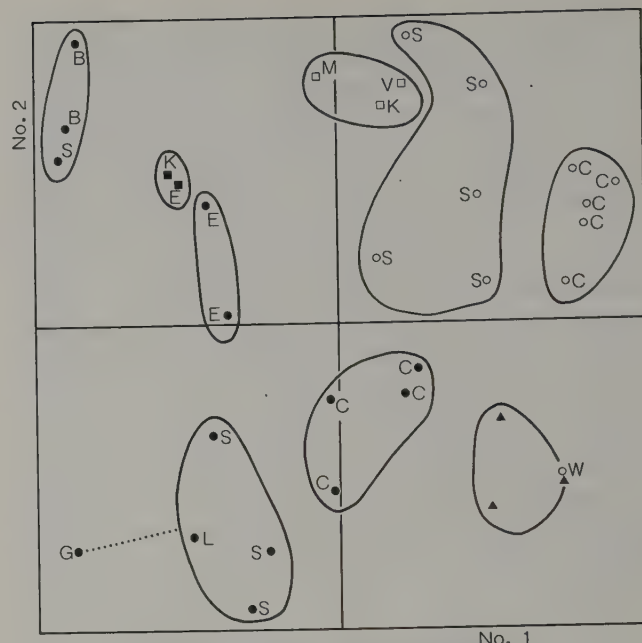


Fig. 4.2 An ordination on first two principal components from nine wing measurements of *Corethrella* (Chaoboridae) spp. Open symbols indicate females, closed ones males; shape indicates species; letters indicate localities. Lines enclose notional clusters. [After Colless 1986: Fig. 70]

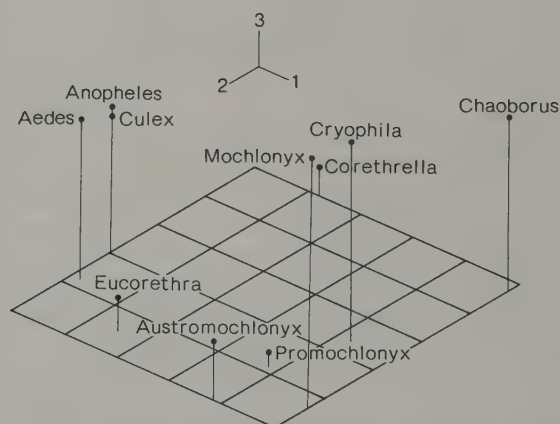


Fig. 4.3 An ordination on first three principal components from seven genera of Chaoboridae and three of Culicidae (*Aedes*, *Anopheles*, *Culex*). Axes shown as insert. [After Colless 1986: Fig. 70]

closest relative. Thus, reconstruction of the phylogeny consists of the search for successive sister groups, through recognition of increasingly more general synapomorphies.

Cladists represent the hierarchical pattern in *cladograms*, which are branching diagrams (e.g. Fig. 4.5). A cladogram reflects character state distributions and systematists often take this to be isomorphic with the putative evolutionary relationships of the taxa, although other interpretation is possible (e.g. Nelson and Platnick 1981). The node (point of bifurcation) in a cladogram represents the homologies shared by taxa united by the node and is not an actual ancestor but may be termed a *hypothetical ancestor*. The term *stem group*, used for example by

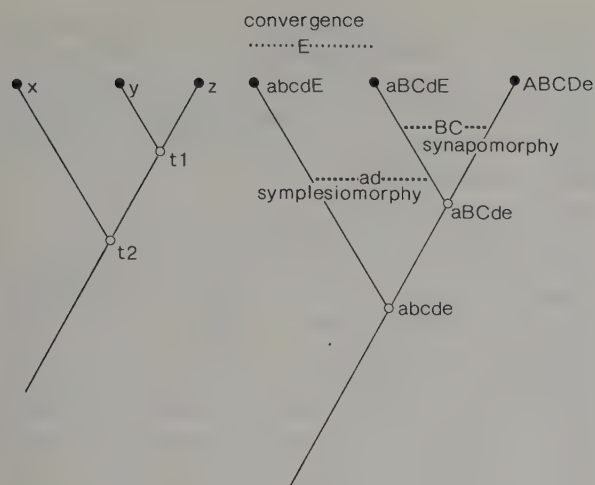


Fig. 4.4 The cladistic concept of relationship.

Left: Species y and z are more closely related to one another than to a third species x if, and only if, z has at least one hypothetical ancestor in common with species y [at t1] that is not also a hypothetical ancestor of x.

Right: The detection of relationship between x, y and z by observation of the distribution of ancestral character states a, b, c, d, e and their derived or advanced homologues A, B, C, D, E in the three species (and inferred in their common ancestors; open circles). *Synapomorphies* such as 'B' and 'C' are shared derived character states, homologues that characterise *monophyletic* groups. *Symplesiomorphies* such as 'a' and 'd' are shared ancestral character states, homologues inherited from a more distant ancestor such that their distribution is wider than the group under study. *Autapomorphies* (e.g. 'A' and 'D' in species z) are unique to a taxon.

The group x + y, characterised by synapomorphies, is *monophyletic*, containing species more closely related to each other than to any outside the group. Non-monophyletic groups such as x + y, if defined by symplesiomorphies are *paraphyletic*; if defined by convergent characters such as 'E', are *polyphyletic*. [After Patterson 1987a]

Kukalová-Peck in Chapter 6, refers to groups of actual organisms belonging to unresolved basal lineages, but does not indicate that they are supra-specific ancestors, a concept rejected by cladists (e.g. Ax 1985). The 'ground-plan' of a group is the set of predominantly plesiomorphic character states that define the basal node of that group.

A hypothetical ancestor and all of its descendants, the products of phylogenesis, form a *monophyletic* group or *clade*. If either a single taxon or larger monophyletic group descendant from a hypothetical ancestor is excluded from a larger monophyletic group, then the residual taxa form a *paraphyletic* group, lacking some descendants of the ancestor. A group that is broader than that derived from a single common ancestor is *polyphyletic* (Fig. 4.4). These terms can be defined in terms of the character states that identify them: a monophyletic assemblage should be united by synapomorphy, a paraphyletic assemblage by only symplesiomorphy and a polyphyletic assemblage by convergent character state(s) (Fig. 4.4). Cladists seek monophyletic groupings by recognition and analysis of apomorphic character states, distinguishing these from homoplasious (non-homologous or convergently acquired) and plesiomorphic states.

Characters and Character Polarity

Early cladists handled relatively few characters and constructed cladograms by hand; many contemporary exponents follow this practice. With the advent of computers, cladistic analyses can now employ many characters utilising the numerical coding methods outlined on p. 115. Cladistics differs from phenetics in considering *polarity* of the states of binary and multistate characters. Several methods for deriving morphological transformations exist, but ascribing polarity, and to a lesser extent assigning order, assumes *a priori* knowledge of the course of evolution, and may prejudice the ability of a subsequently derived cladogram to allow inference of evolutionary pathways. Nonetheless ordering of states need only indicate a logically most probable transformation series and need not specify the direction or the starting point (Thiele and Ladiges 1988) and thus the degree of assumed knowledge need not be large. The treatment of characters with multiple states as *unordered* (non-additive), allows an algorithm to treat any state as derivable from any other.

The assignment of *character polarity*, that is distinguishing derived (apomorphic) from ancestral (plesiomorphic) character states, is crucial to the cladistic method. Hennig (1950, 1966) recommended several ways to polarise characters but the three most widely accepted are outgroup comparison, ontogenetic transformation and the use of fossils. The former two are the most applicable to insects. The outgroup method may be applied *a priori*, with polarity assigned manually before analysis, or *a posteriori*, with polarity indirectly assigned from a clado-

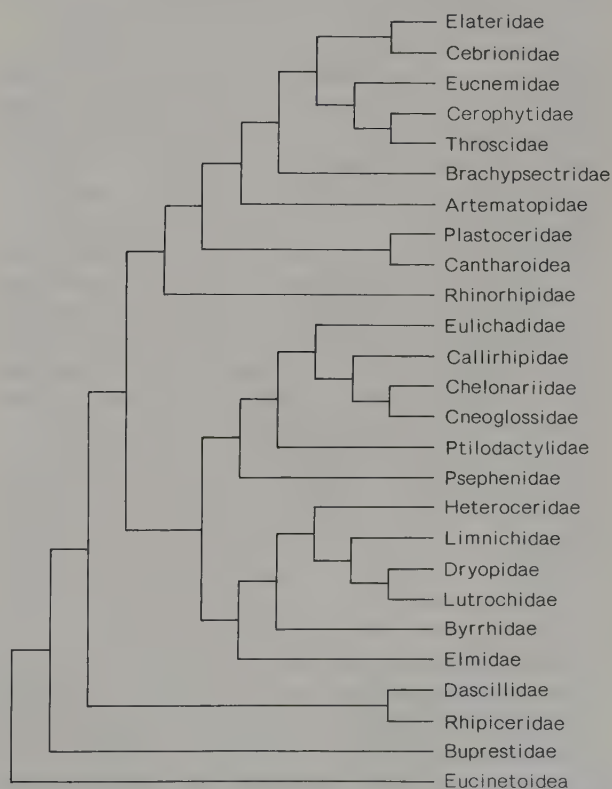


Fig. 4.5 A cladogram (rooted tree) of 26 taxa and 112 characters, rooted to an outgroup, for elateriform Coleoptera. [After Lawrence 1988b]

gram after an algorithm has produced an unrooted tree. In contrast, polarities derived from ontogeny, are applied only prior to analysis.

The outgroup method depends upon comparison of the character states present in the study group (*ingroup*) with those found in progressively more phylogenetically distant sister groups (*outgroups*). Assessment of the polarity of each ingroup character state is made by wider reference, with the assumption that if two states are present, then the state occurring in the outgroup(s) is assumed to be more ancestral (Watrous and Wheeler 1981). Problems that occur when there is more than one outgroup character state have been addressed by Maddison *et al.* (1984). Polarity assignment by the outgroup method assumes some prior knowledge of the phylogeny of the broader group under study and has been criticised for its circularity (Colless 1969a, b). However, phylogenetic hypotheses (perhaps derived from purely phenetic approaches) are available for some groups and sister groups can be determined with some degree of confidence. Nevertheless, in many groups of insects the sister group relationships are unknown and the outgroup method has its limitations.

Ontogeny emphasises the transformation of characters during the growth and development of an individual. Advocates of the primacy of ontogeny in assessing character polarity argue that it requires no prior knowledge of phylogeny (e.g. Nelson 1978a, 1985; Patterson 1982). Although there are differences in interpretation of ontogenetic evidence, the developmental precedence (and commonality) of ancestral states over later and less general derived states is always emphasised (Nelson 1978a, 1985). The general utility of ontogenetic data is restricted by the possibility of deletions and insertions of attributes, including early developmental appearance of derived states and dedifferentiation (Kluge 1985; Kluge and Strauss 1985). Metamorphosis in holometabolous insects clearly complicates ontogeny.

Features from all developmental stages of insects are used increasingly but only Wheeler (1990) appears to have applied ontogeny to deduce phylogeny. The presence of discrete developmental stages (the instars) in hemimetabolous and holometabolous insects (Chapter 2) provides excellent opportunity to test, for example, congruence between phylogenies derived from ontogenetic evidence and those from outgroup criteria, and to examine character homologies throughout life cycles with and without the intervention of metamorphosis.

Palaeontology has made claims to its central position in phylogenetic deduction. Hennig (1966: 95) believed that fossils could be used to determine character polarity with the geologically earliest appearance of a character state being plesiomorphic relative to a homologue appearing later in the fossil record. However, many scientists including palaeontologists (e.g. Patterson 1981a; Forey 1982) express reservations because, although an ancestral character state must precede the derived, the fossil record may not reflect the temporal sequence because of imperfect preservation (Ridley 1986: Fig. 4.12). The paucity of fossil representation and the imperfect nature of preservation, also means that vital characters are obscured or lost.

Patterson (1981a) recognised that the best information attainable from fossils concerns stem groups (see above) which can give additional information concerning recent groupings. Kukalová-Peck (Chapter 6) demonstrates how examination of fossils can lead to reanalysis of character polarity and homology.

Cladogram Construction

A cladogram may be constructed by visual inspection of the data for cases in which relatively few taxa and few characters of unambiguous polarity are assessed. Problems arise when numbers of characters and/or taxa increase. Even under these circumstances, if all synapomorphies covary hierarchically (*i.e.* there is no homoplasy), cladograms can be constructed by hand. However, homoplasy seems to be rampant (e.g. Gauld and Mound 1982) and causes irreconcilable character conflict, as with character e/E in Figure 4.4. Hennig (1950, 1966) and other early cladists did not specify how to deal with intractable conflict beyond urging re-examination of all characters. Farris (1973, reconsidered in 1983) and Sobér (1983) argue that *parsimony* is the only logically defensible means to reconcile conflict in a character data set. The parsimony criterion, that is the restriction of homoplasy by minimising the number of *ad hoc* state changes, is the basis of dendrogram-generating algorithms such as that of Wagner (Wagner 1963; Farris 1970), developed to handle complex data sets. The use of the parsimony criterion does not imply that evolution is parsimonious, only that it is the only means to support one phylogenetic hypothesis over others. In contrast to the parsimonious minimisation of character state changes, *compatibility analysis* minimises the number of mutually incompatible characters (Le Quesne 1982; Meacham and Estabrook 1985).

All algorithms for phylogenetic data analysis involve biological assumptions concerning relative likelihoods of character state changes (reviewed by Felsenstein 1983) and of character correlations. A frequent assumption is that convergence and reversal are equally likely, but restrictions on character reversal may be invoked. Different assumptions affect the resultant cladogram, but the choices have not always been made explicit.

In circumstances where the phylogenetic relationships among taxa are unspecified, an *unrooted* cladogram can be generated. A *rooted* cladogram is produced when ancestral conditions are determined, allowing characters to be polarised. Classifications can be produced best from rooted trees, since in an unrooted tree the number of potential classifications may be as many as there are components, since any can be treated as ancestral.

Evolutionary Systematics

The third and traditional approach has been variously named evolutionary systematics, evolutionary taxonomy, evolutionary classification and phylistics. Explicit justification of evolutionary systematics, for example by Mayr (1965, 1969) and Ashlock (1979), was a response to criticism (e.g. Sokal and Sneath 1963) of the apparent lack of a unified method in 'traditional' taxonomic practice. However, even the proponents of evolutionary systemat-

ics agree that it is an eclectic approach based upon all aspects of evolutionary theory (Bock 1976).

Evolutionary systematists reject the pheneticists' pure operationalism which lacks an explicit evolutionary basis (Mayr 1965), and support the cladists' view that classification should be based on genealogy (Mayr 1981). Cladistic classifications are based entirely on genealogy (*cladogenesis*) and phenetic ones on estimates of morphological divergence (*anagenesis*). In contrast, evolutionary systematists, including Simpson (1961) and Mayr (1969, 1981), stress that neither anagenesis nor cladogenesis alone should be used to produce a classification. The results of evolutionary analysis are incorporated in a *phylogram*, a branching diagram which records both the branching points and the degree of subsequent divergence (Fig. 4.6) (Mayr 1981).

Classification

Classification is the branch of systematics involving ordering the diversity of nature into an effective storage and retrieval system (see p. 109). Although other proposals for classification exist (Dupraw 1965; and see Wiley 1981), virtually all systematists work within the framework of the Linnaean hierarchical nomenclatural system that involves subordination of groups within groups, with the rank shown by the name of the category. However, substantial differences exist concerning what information should be stored and what can be retrieved. These disparities in classification predominantly concern the higher taxonomic levels rather than the discrimination of species.

One major controversy is whether recognition of a pattern of nature is a classificatory end in itself, in effect recognising that many pre-evolutionary classifications

reflected this pattern. This 'process-free' view is held by pheneticists such as Sneath and Sokal (1973) and cladists such as Platnick (1979) and Patterson (1982) (sometimes termed 'pattern' or 'transformed' cladists). In contrast, those with an explicitly evolutionary bias, such as Bock (1976), Mayr (1981), Beatty (1982) and Ball (1983), advocate that classifications should be formulated to reflect what is known of the processes that brought about the natural hierarchy.

A second, related, issue concerns the mechanism for conversion of a dendrogram or 'tree' (phenogram, scatter diagram, phylogram or cladogram) into a classification. There are no criteria for any absolute measurement of taxonomic rank and thus there is considerable room for subjectivity on the part of the systematist. For example, the degree of phenetic difference taken to represent generic or higher rank, even if made explicit, is arbitrary. Likewise, the various conventions used by cladists in assessing categorical limits from a given cladogram and the relative emphasis placed on the degree of anagenesis by evolutionary systematists will affect the ranking in the resultant classifications. Thus, contrary to an often expressed belief (e.g. Colless 1977), systematists of any school may be 'splitters', with a predilection to subdivide taxa, or the converse, 'lumpers'.

Phenetic Classification

The pheneticist must decide how the information depicted in a scatter diagram or phenogram is to be translated into a classification. Explicit statements concerning this process are scanty, but see McNeill (1979a, b) and Colless (in Rentz 1985) for fuller discussion than that given by the early proponents of phenetics. Scatter diagrams are not hierarchical and cannot be readily converted into a Linnaean classification (Sokal 1986). To convert a phenogram into a classification, three factors must be considered: the ordering of the fusions of OTUs, the number of taxa within each cluster, and the internode length or scale (the distance values at which fusions occur). Emphasis of one of these over the others may lead to different ranking within the classification. In practice, the strict use of scale (equating taxon rank with a particular distance value) is rare, but consistent membership of a phenetic group in different analyses (*robustness*) is considered to be of classificatory significance.

Some Australian systematic entomologists have been amongst the foremost proponents of a phenetic approach. Examples of their arthropod studies include Key (1985, Orthoptera), Koch and Colless (1986, Chilopoda) and Colless (1986, Diptera).

Cladistic Classification

The derivation of a cladistic classification from a cladogram can be a direct process following strict guidelines. Only monophyletic groups are named, sister groups are co-ordinate and of equivalent rank, and rank order can be derived directly from the cladogram. Few systematists have produced completely subordinate classifications in which every node is named: this produces an unaccept-

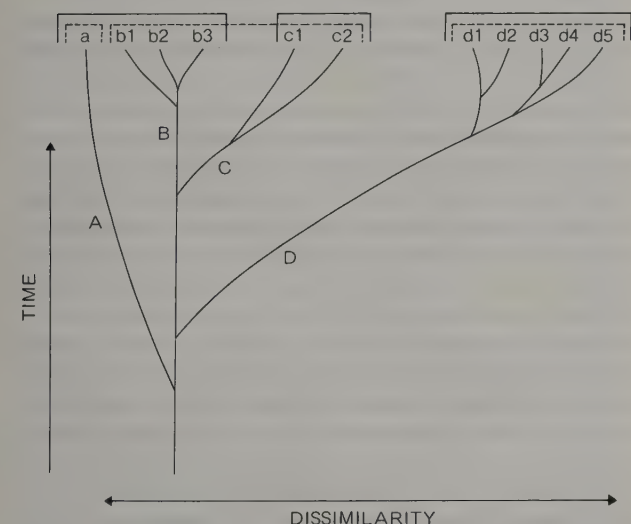


Fig. 4.6 A hypothetical phylogenetic tree (phylogram), illustrating problems of generic classification.

A, B, C, D. Evolutionary lineages through time, terminating in extant species a, b1-3, c1 and c2, and d1-d5.

----- Possible generic limits of a pheneticist taxonomist.

----- Possible generic limits of a cladistic taxonomist

[After CSIRO 1970]

able plethora of categories (Colless 1977). Wiley's (1981) suggestion for an annotated Linnaean classification is a pragmatic alternative. The assigning of absolute rank on the basis of palaeontological age, as suggested by Hennig (1950, 1966), would have profound consequences for the relative ranking of, for example, groups of insects compared with groups of vertebrates and the idea has not been pursued. In practice, some pre-existing framework of higher groupings is accepted and only subordinate categories are derived from the cladogram. A consequence of accepting elements of previous classifications and of adhering to taxonomic conventions within the group under study is the production of both monophyletic and paraphyletic groups in the resultant classification. Cladists endeavour to eliminate or, at least minimise, paraphyly.

Lawrence's (1988b) analysis of the elateriform Coleoptera and J. A. Davis's (1986) psephenid study are two Australian examples that demonstrate the application of cladistic techniques to classification.

Evolutionary Classification

The derivation of evolutionary classifications has been described as eclectic or syncretist, since rigorous rules have not been formulated. Although the cladists' synapomorphic similarity is accepted as a means of deriving genealogy, weighted autapomorphic characters are incorporated in the phylogram and hence the classification. Monophyletic groups with distinctive suites of characters (autapomorphies) frequently are elevated in the taxonomic hierarchy because of these characters, thereby leaving a remnant paraphyletic assemblage. Entomological examples include the dipterous Dolichopodidae versus the paraphyletic Empididae and the odonate Anisoptera versus the paraphyletic Zygoptera.

Classificatory Conclusions

Systematists agree about the desirability of a single classification system but, as seen above, philosophies and methods differ. Assessment of the relative merits of the systematic schools are generally made by reference to the resultant classifications. Ideally classifications should be informative and robust, that is stable when further characters or taxa are added. All schools claim to produce maximally informative or 'natural' classifications (p. 110) and resolution is unlikely while the definitions of these terms remain unclear. The ratio of characters to taxa has a significant bearing on the outcome of most analyses (Sokal 1985) and it is clearly desirable to increase the number of characters when many taxa are studied, irrespective of the method of analysis.

Many entomological classifications are based on adult characters alone, although these would be enhanced by the addition of data from other life history stages. Larvae and pupae do not have a biological existence separate from the adults of their species and are merely alternate expressions of the genotype (Mayr 1965); their phylogenies are identical. Congruence of independently produced classifications from each life history stage greatly increases confidence in a classification in the same way as a con-

gruent classification derived from, for example, a molecular data set.

Discrepancies between classifications based on different life history stages may arise in non-cladistic analyses when evolutionary rates, reflected in anagenesis, differ substantially between stages (Mayr 1965). Since evolutionary rates do vary and furthermore homoplasy can be unevenly distributed between life history stages, incongruence observed in phenetic analyses (e.g. Rohlf 1963; Michener 1977) is to be expected. Highly corroborated cladistic classifications representing cladogenesis alone should be congruent between different life history stages.

Further tests of stability may be made by analysing alternative data sets. Phylogenies derived from molecular data frequently differ from those derived from 'traditional' morphology and it has been suggested (e.g. Lewin 1987) that molecular characters should give better estimates of phylogeny since: (i) these data are derived directly from the genome and (ii) thousands of characters can be obtained by sequencing nucleic acids using sophisticated and increasingly routine molecular techniques. In the past similar views on the superiority of karyotypic or electrophoretic data have been expressed. However, homoplasy is as much a problem in molecular data sets as in any others and difficulties lie in the recognition of homology through the correct alignment of sequences (e.g. Patterson 1987a; Mishler *et al.* 1988; Werdelin 1989). Incongruences between morphology and molecules are not unexpected; neither data set is inherently superior and all approaches should be used (Patterson 1987a; Hillis 1987; Cracraft 1989).

Congruence can be examined by using *consensus* methods. These methods (e.g. Adams 1972; Schuh and Farris 1981; Rohlf 1982) allow systematists to compare trees generated by any method or from any data set and to recognise common components. The degree of conflict between multiple trees being compared will be reflected in the degree of resolution of the resultant consensus tree(s) (e.g. Ward 1985). Alternative approaches applied to the results of cladistic analyses are (i) parsimony techniques applied to the combined data set if the separate data sets produce incongruent trees, or (ii) a successive weighting method (Farris 1969) to generate a single tree if multiple equally parsimonious trees are produced from a single data set. Further investigation into the reconciliation of conflict between data sets is required (Werdelin 1989).

Another poorly investigated aspect of systematics concerns estimating the reliability of trees. Algorithms produce hierarchical structure independent of the confidence in the data set. Felsenstein (1985) recommends resampling characters in a 'bootstrap' technique of Penny and Hendy (1985) to give estimates of confidence levels in phylogenies, a technique modified by Sanderson (1989). Faith (pers. comm.) recommends comparative evaluation using a Monte Carlo approach in which character states are randomly reassigned to taxa to give probability values to tree topologies.

A preferred hypothesis of phenetic or phylogenetic relationship may be scarcely more justifiable than others

and, especially in the absence of significance tests, nomenclatural stability must be considered if the new classification differs from that in existence. Classifications do not serve the sole function of conveying information about either similarity or descent. The scientific public and laypersons alike require names (especially the binomen, see below) to access all information ever acquired concerning the taxon. Alteration of a binomen, either for reasons of phylogenetic hypothesis or historical nomenclatural rectitude (see 'Principle of Priority', p. 122), may lead to loss of the connection between the species and some or all biological information associated with it. If there is an established classificatory framework, as is true for most organisms, existing names and concepts should not be discarded lightly.

ZOOLOGICAL NOMENCLATURE

Unambiguous communication of biological information requires consistent names for the millions of extant and extinct species and their higher groupings. Vernacular (common) names must have existed since humans first spoke, but most linguistic groups use different names for the same animals. Vernacular names (e.g. Carne 1987) have a useful function, but taxonomy is international and thus a nomenclatural system must be universal and names should be cited in an internationally acceptable language. Furthermore, the system must promote nomenclatural stability, so each taxon will be known by a unique and preferably unchanging name. There should be a permanent link between each name and the particular taxon to which it refers, and the rank of the taxon should be recognisable from each name. Procedures should exist to accommodate changing concepts of the limits, rank and status of particular taxa and distinguish valid from invalid nomenclatural actions. These requirements are met by universal rules which stipulate how zoological taxa should be named and how infractions should be dealt with.

The existing nomenclatural system that replaced all previous schemes was founded by Carolus Linnaeus, who first consistently used a binominal system of generic plus specific names. Zoological nomenclature dates from 1 January 1758 when the 10th edition of Linnaeus's *Systema Naturae* was published. Older names are disregarded.

The rules associated with this system were not formalised until the first *Règles Internationales de la Nomenclature Zoologique* was published in 1905, by which time post-Linnaean zoological nomenclature was in great confusion. Early versions of the rules gave only general guidance, but later editions of the *International Code of Zoological Nomenclature* became all-encompassing, authoritative and indispensable to taxonomy. The Code is concerned only with nomenclature; it does not restrict the freedom of taxonomic judgement. Its force derives only from a consensus of zoologists being willing to accept its authority. It is periodically updated, amended and improved under the jurisdiction of the International Commission on Zoological Nomenclature.

The International Code of Zoological Nomenclature

The 3rd edition of the *International Code of Zoological Nomenclature* (1985) includes a preamble followed by 88 articles grouped in 18 chapters. The articles consist of mandatory provisions (some operational only from specified dates), often accompanied by non-mandatory *recommendations* that suggest procedures for situations not covered by specific articles. There are several appendices with the force of recommendations, including a 'Code of Ethics', and a glossary defines terms. The Code is published in parallel, fully equivalent, official English and French texts. Cogger (1987) gives a succinct summary of the 1985 Code.

Relevant taxonomic categories are treated in three groups: the *species group* (species and subspecies), *genus group* (genus and subgenus) and *family group* (all ranks from superfamily to subtribe). Within each group, names are *coordinate*, that is, they are subject to identical rules. Names of taxa above the family group and those applied to hybrids and infrasubspecific entities are not covered by the Code.

Formation of Names

All zoological names must be Latin or latinised and must be capable of being treated as Latin if formed from other words, as for example, when Rentz (1985) used an Australian Aboriginal adjective for beautiful, 'amaroo', and the Aboriginal tribal name 'Narranga' as specific names in the orthopteroid genus *Glenbalodectes*. Names cannot include numerals, diacritic marks, apostrophes or diaereses, and hyphenations are rarely allowed. Names of the genus and species groups should be printed in distinctive type, usually italics. The names of the original describer(s) (*author(s)*), which may be abbreviated, and the original publication date, may be cited but are not parts of scientific names. When a species-group name is combined with a generic name different from the original placement, the author's name is enclosed in parentheses. In taxonomic publications, the author's name (and year of publication where relevant) should be indicated on the first citation of genus, species and subspecies.

Species-group names must consist of a word that is, or is treated as, either (i) an adjective or participle in the nominative singular agreeing in gender with the generic name with which it is at any time combined; (ii) a noun in the nominative singular standing in apposition to the generic name; (iii) a noun in the genitive case; or (iv) an adjective used as a noun and derived from the name of another organism with which the species is associated.

Genus-group names are nouns in the nominative singular, or are treated as such, with an initial capital letter. The species name or *binomen* (the name of a species) is the combined generic and specific name. Specific names, the second name in a binominal or trinominal combination, can be used formally only in combination with a generic name which may, after first citation in full, be reduced to its initial letter. Subgeneric names are not obligatory but, if cited, are in mandatory parentheses between generic and specific names, e.g. *Aedes* (*Finlaya*)

notoscriptus. A subspecific name is the third name in a trinominal combination.

A species-group name in parenthesis may follow a genus-group name or stand between a genus-group name and a specific name to denote an aggregate of species, e.g. *Amblyopone (australis complex)*, *Amblyopone (australis) leae*, or after the specific name in a trinomen to denote an aggregate of subspecies.

Family-group names must each be based on the stem of the name of an included genus. A suffix is added indicating the rank of the taxon; these are indicated in Table 4.1 (p. 109). These names are plural in form and take an initial capital letter except when colloquial (e.g. Scarabaeidae: scarabaeids; Melolonthinae: melolonthines, etc.). Nomenclature above the family group is not covered by the Code, but conventions apply. Names are capitalised, latinised plurals without standard suffixes and written in Roman type.

The Principle of Priority (see below) applies in the selection of interpolated names. A term indicating the meaning of the interpolated name should be included in the same parentheses on the first use of the notation in any work (e.g. 'superspecies', 'complex', 'species group', etc.).

Availability of Names

To be established for use (*available*), newly proposed names must satisfy various requirements of the Code. The chief of these are that the names must have been (i) correctly formed (certain infractions do not prevent availability from the original author and date, but must be corrected), (ii) published in accordance with a detailed definition of publication, and (iii) accompanied by a definitive description. Slightly different rules apply before 1931. In the case of a genus-group name published after 1930, a type species (see below) must have been correctly fixed. An unavailable name is termed a *nomen nudum*, but a name may be available for nomenclatural use even when it is 'invalid' (see below).

The Principle of Priority

Although each taxon governed by the Code can have only one scientifically correct (*valid*) name, additional names (*synonyms*) often come to be applied to the same taxon. Synonyms arise when an already described taxon is inadvertently renamed, or when two or more supposedly distinct and separately named taxa are shown to be identical. The Principle of Priority prescribes that the valid name is the one with the earliest date of publication as an available name (the *senior synonym*). Others are *junior synonyms* (invalid names) and 'enter into synonymy' with the senior name. A junior synonym remains available and may be reinstated if it is found to refer to a separate coordinate (belonging to the same categorical group) taxon, or if its senior synonym is invalidated. Between coordinate taxa the priority of a name is not affected by elevation or reduction in rank, as when a subspecies is elevated to a species or a genus reduced to a subgenus.

The Principle of Homonymy

When two or more independently published available names with identical spelling are applied to different taxa of the same rank they are termed *homonyms*. The Principle of Homonymy requires rejection of the junior homonym and either its replacement by its oldest available synonym or, if none exists, a new name—a *nomen novum*—must be provided. Homonyms of species-group names may be 'primary', as when a name is published for a new species or subspecies when an identical name is already in use for another taxon in the same genus, or 'secondary', as when two or more identical specific names, originally described in different genera, are brought together under the same generic name. The latter may occur as a consequence of the synonymy of the genera in which they were previously included, or by shifts of species between genera due to changes in their classification. A junior primary homonym must be permanently rejected; a junior secondary homonym must be rejected by those who believe that the taxa involved are 'congeneric', but not by those who do not (for this reason rival combinations can be current if taxonomists disagree on classification). Certain minor variant spellings are disregarded in determining whether species-group names are 'identical'.

If nomenclatural actions involving synonyms or homonyms are published on precisely the same date (regardless of authorship or place) their precedence is determined by the 'first reviser' to publish an unequivocal choice. Although it is sometimes assumed that the earliest description in the text ('page priority') takes precedence, this is not a requirement of the Code.

Types

A permanent link between each scientific name and the taxon to which it refers is established in taxonomy by the use of 'types'. A species described as new to science will always be based upon one or more specimens comprising its *type series*. If the type series consists of a single individual, this is the *holotype* of the new species by *monotypy*; if there are several specimens one (and only one) should be clearly designated by the author as the holotype. The holotype of a *nominal species* (a nomenclatural concept) provides the objective international standard of reference whereby the application of that name is determined. The specimen need not be 'typical' of the species in any normal sense; its only purpose is to certify that the name it bears applies to the biological species of which it is a member. If no holotype was designated by the original author(s) but the type series can be recognised, for example from the original publication and/or specimen labels, its members are *syntypes*. A taxonomist may subsequently select one syntype as the *lectotype* and the first such designation must be accepted. To be valid, a lectotype designation must be published; it is not a house-keeping task but should be part of a revisionary study. However, the lack of a holotype or lectotype is not a problem necessarily requiring rectification. If for any reason no original material exists then a *neotype* may be des-

ignated, although exacting conditions prevail in these cases. Lectotypes and neotypes are exactly equivalent to holotypes and these three plus syntypes comprise the set of 'name-bearing types'.

Name-bearing types should be labelled unmistakably and lodged in an appropriate museum or similar public institution where they will be held in trust for science and made available to the scientific community.

The type concept allows recognition of species new to science (colloquially 'new' or 'undescribed' species) when comparison of newly acquired material with types shows differences judged to be of specific significance. Conversely, confident identifications are made when material is compared with name bearing types and is judged to be conspecific.

Specimens in the type series in addition to the holotype are *paratypes*; *paralectotypes* are specimens remaining from the type series after a lectotype is designated. Paratypes and paralectotypes might not represent the same species as the associated name-bearing type, and therefore are no more than specimens identified by the original author. Other type terms (e.g. allotype, cotype, topotype) have been used but have no nomenclatural status and are subject only to recommendations in the Code.

The type of a genus or subgenus (the *type species*) is not a specimen but an included species. If only one species is assigned to the taxon by its author, that is its type species by monotypy. Since 1930 the fixation of a type species for genus-group names has been a legal requirement to make the name available. The Code specifies how type species should be selected if none was designated for a genus-group name published before 1931. The type species is the objective standard of reference determining application of a genus-group name. Generic or subgeneric concepts may alter, but the type species must always follow the name of the taxon. The type of a taxon in the family group is a genus, the *type genus*, and is defined as that genus whose name is incorporated in the name of the family-group taxon.

The type of a given taxon is automatically the type of any taxon based on the same name in the same co-ordinate group. If two different *nominal taxa* (nomenclatural concepts) have the same type, they must be *objective synonyms*, whereas if two nominal taxa have different types but are considered to be synonyms, they are *subjective synonyms*. There is no type system above family-group names, priority is only loosely recognised but homonymy is rectified.

The *type locality* is the geographical place of collection of a name-bearing type of the species group. In palaeontology, the *type horizon* is the geological stratum of the collection. If a host association is relevant, a *type host* may be recognised.

The International Commission on Zoological Nomenclature (ICZN)

Despite the comprehensive guidance of the Code, cases may arise for which correct procedure is open to doubt. To meet such situations, authoritative guidance to interpretation of the Code may be sought from the ICZN.

There is in general no 'case-law': each decision refers to a single case and does not stand as a precedent. Many names that prove to be invalid under the Code have been in long-term general use, sometimes for important and frequently cited taxa. Disruptive name changes should be avoided: the ICZN can suspend the Code in relation to particular cases and rule in favour of 'usage' against change. The Code requires that in cases in which application of the Principle of Priority would upset a long accepted name taxonomists should maintain existing usage and refer the case to the ICZN.

Literature Relevant to Nomenclature

The literature pertaining to nomenclature is especially important to taxonomy because of its scope, archival nature and volume. Details of submissions, and the decisions of the ICZN, are published as 'Opinions' and 'Declarations' in the *Bulletin of Zoological Nomenclature*. Names validated by the ICZN are placed on one of three *Official Lists of Names in Zoology*, one each for species-, genus- and family-group names. There are corresponding *Official Indexes of Rejected and Invalid Names*, and equivalent registers for whole works declared 'rejected and invalid', or approved as available for zoological nomenclature. Independent codes exist for botanical, bacteriological and viral nomenclature; these are reviewed by Ride and Younès (1986). Other important works include generic nomenclators, such as that of 'Neave's' *Nomenclator Zoologicus* (published in seven volumes, the last edited by Edwards and Ververs, 1975), and the *Zoological Record*, which is a comprehensive abstract of all taxonomic works published in a given year.

METHODS OF IDENTIFICATION

There are two means by which insects are identified: the use of keys and descriptions or comparison with reference specimens. One of the functions of the taxonomist is to provide the means for others to correctly identify organisms, through the production of illustrated descriptions and keys. The style and content of descriptions varies with different taxonomic groups, but should be concise, telegraphic, diagnostic and well illustrated. Illustrations may be line drawings or photomicrographs, including scanning electron micrographs, of whole insects and/or selected characters.

Identificatory keys also vary in style and in accordance with user requirements, but are predominantly, as in this book, based upon following a dichotomous series of choices until a single taxon remains. Pictorial keys are becoming more frequent (e.g. E. G. Matthews 1980–1987 for Coleoptera) especially where non-specialist users predominate (e.g. for mosquitoes). The future will see increased 'user-friendliness' with more computer-based interactive expert system keys, such as those using the DELTA, PANKEY (Dallwitz and Paine 1986; Pankhurst 1978) and PESTKEY (Bishop *et al.* 1989) programs. These expert systems depend upon a complete data matrix with multiple access, whereas the user of a dichotomous key is restricted to following the format of

the key and accesses limited data via the key. For this reason identification from conventional keys must be confirmed by comparison with a description or a *diagnosis*. A diagnosis is the formal statement of the character states which distinguish one taxon from others, in contrast to a description which is a full account of the recorded character states of that taxon.

In the construction of a key, character states used should apply to all included individuals, should be relatively constant, should be absolute, or at least quantified rather than relative, and preferably should be based upon readily observable features. Even if these strictures are followed, problems can be encountered in the use of keys. Firstly, the taxon may be more variable, e.g. through geographic variation, than the compiler of the key appreciated. Secondly, the user may fail to recognise polymorphism due to developmental stage or sex. Thirdly, the taxon requiring identification may not have been included, because it was undescribed or regionally unknown when the key was produced.

Under the circumstances prevailing in entomology in which many taxa are indeed undescribed, 'natural' keys (those reflecting branching sequences of postulated phylogenetic relationships, see p. 118) are more likely to allow a sensible approximation. In contrast, 'artificial' keys, based on characters of convenience, may not produce useful results with undescribed taxa and are more

valuable with fully known faunas. In practice, most keys are artificial to some extent. The high frequency of polythetic insect taxa (defined on multiple character states, none of which individually is diagnostic) means that construction of monothetic keys (containing uniquely diagnostic characters) is rarely possible.

Alternatively, or as confirmation of a key-based identification, direct comparison may be made with named insects in collections. Many such collections held in museums, universities and government research institutions are listed by Arnett and Samuelson (1986). For those without access to such comparative collections, confirmation of uncertain identifications attained by means of the literature may be obtained by consultation with an appropriate specialist. A list of Australian taxonomists, their specialities and willingness to accept unsolicited material, is maintained by ABRS and other countries have similar schemes.

For scientists requiring identification input into their research, appropriate specialists should be consulted in advance, consent requested and costs of taxonomic services built into funding applications.

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Phylogeny of Extant Hexapods

N. P. KRISTENSEN

Assessments of the affinities and interrelationships among extant hexapods can be based on comparisons which utilise a wider range of features than those provided by fossil forms (see Chapter 6). In 'easy' cases where genuine synapomorphies abound and homoplasies are few or absent, interrelationships between extant orders can be identified with a degree of certainty unattainable for fossil taxa. However, increasing the amount of available comparative data does not always lead to ease in phylogenetic decision-making. There are cases where the limited number of characters available to the palaeontologist appear to support only a single phylogenetic pattern, yet, when additional characters are studied in extant forms, their derived states are found to be distributed in a more reticulate way. The neontologist thus finds the issue complicated by evidence for a variety of possible phylogenies, of which only one can be true. On the other hand, neontologists, seeing similar modifications in all extant taxa of a particular group, can be led to believe that these modifications arose as a single evolutionary event. If the fossil record shows that extinct members of the group lacked these modifications, then it may be that the neontologist's phylogenetic model is oversimplified and the modifications arose more than once.

This chapter considers the evidence bearing on the phylogenetic (i.e. cladistic) classification of the extant hexapod taxa generally ranked as orders. These taxa are not equivalent either in geological age (i.e. the age of the last common ancestor of the Recent members), or by a criterion relating to branching sequence in the genealogical tree; ranking has been a matter of convention. The extant hexapod orders are mostly entities that have long been recognised as 'distinct' and have proved to be

cladistically well circumscribed, i.e. they have distinct groundplan autapomorphies in at least one developmental stage. Difficulties in assigning a Recent hexapod to order may be due to a primary absence of ordinal autapomorphies in the stage (or sex) of the specimen at hand, or it may be due to secondary modifications (including regressions, such as those associated with loss of feeding or flight) that have obliterated the autapomorphies. A practical key to the extant hexapod orders is presented in Chapter 1.

Considering the huge number of new hexapod species that are continuously being described, and also considering the number of new taxa of high rank that have been discovered during the last fifty years in the comparatively small fauna of marine animals, it is surprising that, since the description of *Grylloblatta* in 1914, all subsequently discovered Recent hexapods have been referable to known orders. However, reservations may be made concerning the bristle-tail genus *Tricholepidion* (described in 1961) and, more questionably, the scorpion fly family Nannochoristidae (described in 1917), as discussed below.

Comprehensive treatments of hexapod phylogeny, which collectively provide entry into the extensive literature on the subject, are given by Boudreaux (1979), Hennig (1981) and Kristensen (1975, 1981). A proposed phylogeny of the major groups of extant Hexapoda is given in Fig. 5.1.

THE MONOPHYLY AND AFFINITIES OF THE HEXAPODA

The superclass Hexapoda comprises the Collembola, Protura, Diplura (*s.l.*), Archaeognatha, Thysanura *s.str.* (= Zygentoma) and Pterygota. The monophyly of this

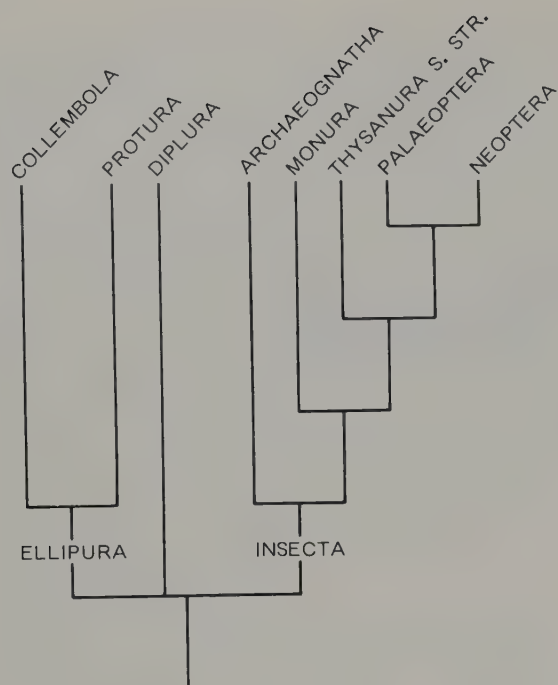


Fig. 5.1 Proposed phylogeny of the major groups of extant Hexapoda.

assemblage of arthropods is inferred primarily from the unique type of tagmosis shared by its members. The hexapod head is composed of a pre-gnathal region (the segmental composition of which remains debatable), the mandibular segment and two postmandibular segments, of which the posterior has the appendages medially fused to form the labium. Of crucial significance is the differentiation of the postcephalic thorax, comprising three segments with relatively large locomotory limbs. The hexapod abdomen is generally believed to be primitively twelve-segmented (eleven genuine metameres plus the telson), so an *ad hoc* explanation (e.g. arrested anamorphosis) is needed in the case of the Collembola, which have only six segments. The limbs on abdominal segments 1–9, when retained, are consistently smaller and weaker than those of the thorax, and it is suggested (Kukalová-Peck 1987 and Chapter 6) that more of their basal segments are incorporated into the abdominal wall than is the case in the thorax. Segment 10 was probably always devoid of limbs. Recent reassessments of the affinities of the Diplura raise doubts about the ancestral configuration of the limbs of segment 11, the cerci (see below).

The ommatidial structure of the faceted eyes of Archaeognatha, Thysanura *s.str.* (Fig. 5.2) and lower Pterygota and of the 'dispersed faceted eyes' of Collembola is strikingly similar, and it is straightforward to consider the presence of two 'primary pigment cells' (derived from corneagenous cells) to be an autapomorphy of the hexapod groundplan (Paulus 1979). The extant Diplura and Protura are secondarily eyeless.

It has been commonplace to consider the small complement of leg segments (coxa, trochanter, femur, tibia, tar-

sus, pretarsus) to be another hexapod autapomorphy (Boudreaux 1979), but Kukalová-Peck (1983, 1987 and Chapter 6), based on conditions in numerous fossils and in some extant hexapods, attributed another four segments ('epicoxa', 'prefemur', pretibial 'patella', 'basitarsus') to the groundplan of the 'free limb', thereby rendering the segment number identical to that in Palaeozoic Myriapoda-Diplopoda. The morphological significance of these leg sections remains debatable, but at least the tight union of the patella and tibia may be upheld as a hexapod autapomorphy in thoracic leg configuration.

Previously identified hexapod autapomorphies in sperm ultrastructure (Jamieson 1987) are now rendered uncertain by the above mentioned reservations concerning dipluran affinities.

When evaluating the arguments presented for the monophyly of the Hexapoda it is important to note that there seems to be no conflicting evidence in the form of likely synapomorphies between one (or more) hexapod subgroup(s) and other non-hexapod arthropod taxa.

For several decades there has been near-universal agreement that the closest relatives of the Hexapoda are

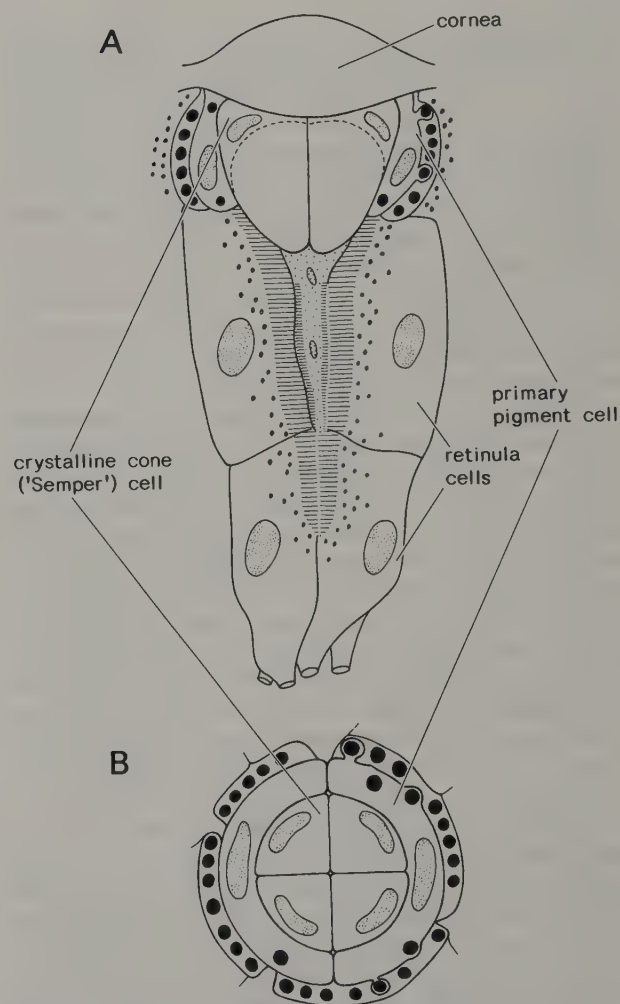


Fig. 5.2 Ommatidium of a lepismatid silverfish (*Thysanura*): A, longitudinal section; B, transverse section. [After Paulus 1979]

to be sought among the myriapods. The two groups share three presumably derived features: presence of anterior tentorial arms, absence of distinct appendages on the tri-tocephalic head segment, and absence of pretarsal levator muscles. The hexapod/myriapod mandible lacks a palp (telopodite). Manton (1972, 1977) insisted that the mandible is actually formed by the whole limb, contrary to the gnathobase mandible of Crustacea; however, as noted by Lauterbach (1972b) and Boudreaux (1979) there seems to be no compelling reason for this. Malpighian tubules and water-absorbing limb-base vesicles are further possible hexapod/myriapod synapomorphies, but then repeated independent reduction of these formations must have taken place in both lineages. The assemblage of myriapods plus hexapods is currently known as the 'Atelocerata', referring to the lack of the second antennae, or as the 'Antennata', which is an unfortunate name when thus restricted, since 'antennae' (one or two pairs) are of much wider occurrence in arthropods. Another name for this assemblage is the 'Tracheata', referring to the general occurrence of tracheae; but, because of the diversity in the topography of spiracles in myriapods and entognathan hexapods, it remains very questionable whether development of a tracheal system was a single event in the evolution of the myriapod/hexapod lineage.

Few zoologists would contest the notion that hexapods descended from a largely homonomously segmented arthropod which would be phenetically classified as 'a myriapod', and it remains a pertinent question whether the known, or at least the extant, 'Myriapoda' are paraphyletic in terms of the hexapods. Dohle (1980) believed that they are, but at the same time underscored the problems inherent in accepting any of the suggested, derived similarities between hexapods and the myriapod subgroup 'Progoneata' (i.e. the Symphyla + (Paupoda + Diplopoda)) as genuine synapomorphies. Boudreaux (1979) on the other hand favoured a genuine sister-group relationship between the Hexapoda and a monophyletic entity Myriapoda, and perhaps at least the peculiar, 'swinging' anterior tentorial arms, serving the mandibular abduction, can be regarded as a groundplan autapomorphy of the latter. In any case there is no longer any support for the once widely favoured theory of a close relationship between the Symphyla and the Hexapoda (or part of the Hexapoda).

Manton (numerous publications, reviewed 1977) insisted that the Onychophora belong to the same assemblage, the 'Uniramia', as the myriapods and hexapods. She believed that the Myriapoda and the Hexapoda are monophyletic entities, but she attributed to the groundplans of both a multi-legged trunk and lobopodial limbs. Manton also asserted that the extant primary hexapod lineages (she treated the Archaeognatha and Thysanura *s.str.* (= Zygentoma) collectively as 'Thysanura', thus recognising only five lineages) had evolved independently from the multi-legged lobopod ancestor, even though she admitted the possibility that the Pterygota and 'Thysanura' are both descended from a very early, common stage (1977: 284). Manton's functional-morphological approach to elucidating arthropod evolution has attracted considerable atten-

tion, but she did not adopt strict cladistic methodology, and her phylogenetic reasoning has been criticised repeatedly on general grounds (e.g. Siewing 1960; Kristensen 1975, 1981; Patterson 1978; Platnick 1978). The relationships she refuted were largely ancestor-descendant relationships between known taxa (often extant ones) for which ancestor-descendant relationships would never be postulated by modern cladists anyway. On the other hand she paid insufficient or no attention to the properties of those hypothetical ancestors that are postulated in the course of any cladistic analysis. There still does not seem to be any compelling evidence against the straightforward notion that the last common ancestor of the hexapod lineages was itself a hexapod arthropod. As far as the Onychophora are concerned, it does seem questionable whether synapomorphies between these animals and the Atelocerata can be identified in the definitive body structure. According to D. T. Anderson (1973, 1979) similarities in the embryonic fate maps of onychophorans and atelocerates support the monophyly of the 'Uniramia', but the significance of this embryological evidence has been questioned by Weygoldt (1979) who, along with Boudreaux (1979) and Lauterbach (1980), favours the conservative view, that the closest extant relatives of the Atelocerata are the other 'mandibulate' arthropods, i.e. the Crustacea. The monophyly of the 'Mandibulata' is also supported by the extraordinary similarity of the ommatidia of the compound eye in the groundplans of the Crustacea and Hexapoda; myriapod eyes can plausibly be interpreted to be secondarily modified (Paulus 1979).

THE ENTOGNATHAN HEXAPODS

The Collembola, Protura and Diplura have had a chequered history in systematic entomology. Much attention has been paid to the phenetic gaps that separate these three taxa from each other and from the remaining hexapods, here called the Insecta, and they have sometimes all been ranked as independent classes. But during the last few decades the view has been widely adopted that they might constitute together a monophyletic class Entognatha, which has a sister-group relationship to the remaining hexapods, the class Insecta. Within the Entognatha a sister-group relationship has been recognised between the Diplura and a superorder Ellipura comprising the Protura + Collembola (Tuxen 1959, 1970a; Lauterbach 1972a; Kristensen 1975, 1981; Boudreaux 1979; Hennig 1981). Alleged autapomorphies that have been attributed to the groundplan of the Entognatha include primarily 'entognathy' itself: the more or less extensive overgrowth of the mouth-parts by 'oral folds' from the lateral cranial wall, whereby the basal parts of the mandibles and maxillae come to be located in 'gnathal pouches' (Fig. 5.3). Moreover, the Malpighian tubules are reduced and the compound eyes are degenerate in the Collembola (Paulus 1972, 1979) and entirely lacking in extant Diplura and Protura. The absence of a centriole adjunct from entognathan sperm has tentatively been considered apomorphic, since this formation occurs in some myriapods as well as in insects (Jamieson 1987).

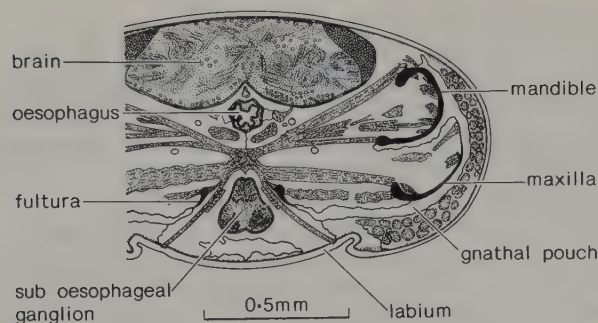


Fig. 5.3 *Heterojapyx evansi*, Diplura, transverse section of head showing entognathy. [From preparation by B. J. Bancroft]

Manton repeatedly asserted that entognathy had arisen independently in the three entognathan orders, but the phenetic differences to which she alluded have been considered unconvincing evidence (Kristensen 1975, 1981). However, new data on fossil and Recent Diplura (Kukalová-Peck 1987 and Chapter 6) necessitate a reassessment of the status and affinities of this taxon. Conditions in the U. Carboniferous *Testajapyx* (Fig. 6.8), whose assignment to the japygid lineage seems well founded, demonstrate not only that the absence of eyes must be discarded as a dipluran autapomorphy, but that a partially degenerate compound eye was part of the entognathan groundplan. Similarly, the relatively long and multiarticulated maxillary and labial palps of *Testajapyx* demonstrate that the extreme palp reduction seen in extant entognathans cannot be a groundplan autapomorphy of the group as a whole.

According to Kukalová-Peck it is a synapomorphy of the Diplura and the non-entognathan hexapods that the abdominal limb bases, inclusive of the trochanter, have been incorporated into the abdominal wall, whereas, in the groundplan of the Collembola + Protura assemblage only the subcoxa has been incorporated; this interesting suggestion awaits further documentation and evaluation. But the suggestion that the closest relationships of the Diplura are with the non-entognathans naturally leads to a reconsideration of the significance of two characters that have previously been considered autapomorphic of the hexapod groundplan and secondarily modified in the Collembola + Protura, viz. the filiform cerci and details of axoneme structure in the sperm.

The cerci, i.e. the limbs of segment 11, are phylogenetically enigmatic structures. They are filiform in Diplura-Campodeidae (shortened or forcipate configurations in other Diplura generally are considered secondary), in Archaeognatha, Thysanura *s.str.* and primitive pterygotes, and it has therefore seemed straightforward to attribute filiform cerci to the hexapod groundplan. Viewing this character in isolation it would, of course, be more parsimonious to consider it synapomorphic of the Diplura + Insecta only, thereby obviating the need for postulating a secondary reduction in the Collembola + Protura. However, the issue is further complicated by the finding (Kukalová-Peck 1983, 1987 and Chapter 6) that in the

Palaeozoic Monura apparent segment 11 limbs are basically similar to the rather short preceding abdominal limbs and have retained paired claws. If these limbs do indeed pertain to 11, and if it is correct (as inferred from mandibular structure and gonangulum development, see p. 150) that the Monura have a sister-group relationship to Thysanura + Pterygota, then the filiform cerci must have been developed independently three times. This would be in accordance with another recent finding (E. L. Smith, see Kukalová-Peck 1987) that the cercal base is differently developed in the Diplura, Archaeognatha and Thysanura + Pterygota (Kukalová-Peck's Cercofilata).

Sperm evolution of the basic hexapods is discussed in detail by Jamieson (1987). A sperm axoneme with a ring of nine doublets surrounding a central pair of tubules (i.e. the '9+2' pattern) is plesiomorphic within the Arthropoda. Collembola have a 9+2 pattern. Protura lack the central tubules and can have axoneme patterns such as 12+0 or 14+0 (Baccetti 1979). The Diplura-Campodeidae, like the Archaeognatha, Thysanura *s.str.* (Fig. 5.4B) and most Pterygota have a ring of nine single tubules peripheral to the nine 'doublets' of the basic sperm axoneme, leading to the formation of a '9+9+2' configuration, which has been attributed to the hexapod groundplan. If a 9+9+2 configuration is part of the hexapod groundplan, then the patterns in Collembola and Protura would have to be the results of secondary reductions. In mature sperm of campodeids and archaeognathans (Fig. 5.4A) the peripheral singlets become

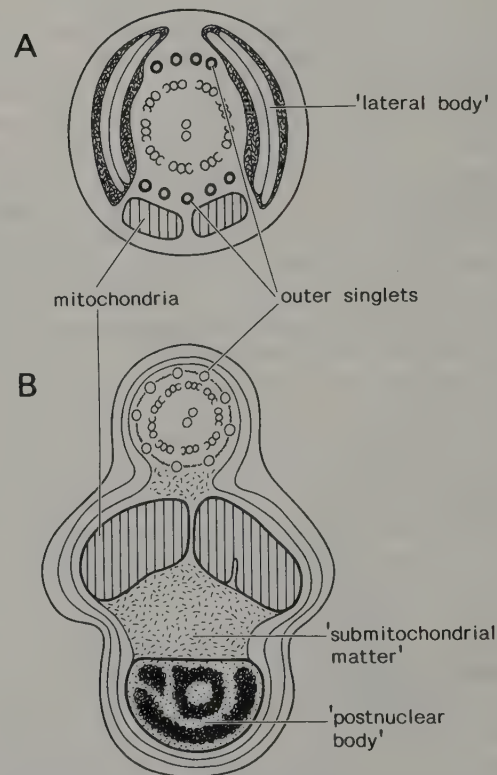


Fig. 5.4 Spermatozoa sectioned transversely behind nucleus: A, Machilidae, Archaeognatha; B, Lepismatidae, Thysanura. [After Wingstrand 1973]

arranged into two groups (of four and five respectively). The 9+9+2 type could alternatively be considered synapomorphic of the Diplura + Insecta, obviating the need for postulating a secondary reduction in the Collembola + Protura. A postulate of this kind would still be necessary to explain the 9+2 pattern of Diplura-Japygidae. In japygids there is a peripheral group of five tubules, which Kristensen (1981) considered to be the counterpart of the peripheral five-tubule group in campodeids-archaeognathans; this suggestion is discarded by Jamieson because of different developmental origins of the tubules. If the unique campodeid/archaeognathan similarity in peripheral-tubule asymmetry is intriguing, a unique campodeid/thysanuran similarity in flagellum insertion in the base of the acrosome is no less so—both cases would seem to be parallelisms. Counterparts of the myriapod 'Tömösvary's organ' are retained on the head of Collembola ('postantennal organ') and Protura ('pseudoculus') (François 1969); their absence in Diplura and Insecta might be considered synapomorphic.

Considering the reticulate distribution of the apomorphies linking the Diplura with other hexapods it is suggested at present to recognise two entognathan classes: the Diplura and the Ellipura (= Parainsecta, = Collembola + Protura) and to present their relationship to the true insects as an unresolved trichotomy. It should be noted that Kukalová-Peck (Chapter 6) includes the Diplura within the Insecta.

Class ELLIPURA (PARAINSECTA)

Body size small (8 mm or less). Entognathy advanced; oral folds almost or actually meeting posteromedially, maxillary palps small (3 segments or fewer) and labial palps minute (1-segmented) when discernible. Posterior/ventral surface of head with median 'linea ventralis', a groove with one or more longitudinal crests, extending from the openings of a set of labial glands backwards onto the neck membrane in the Protura, and even to the preabdominal ventral tube in the Collembola (François 1969). 'Epipharyngeal ganglia' (masses of sensory and secretory cells) enlarged (François 1969). Pretarsal claws unpaired.

The two orders included here both have striking autapomorphies and hence are phenetically distinctly set apart from each other as well as from other hexapods, but on the basis of the preceding putative synapomorphies the monophyly of the Ellipura is here upheld. The interpretation of an unpaired claw as apomorphic at the basic hexapod level is debatable (see Kristensen 1981). Absence of abdominal spiracles has been considered another ellipuran autapomorphy and may indeed be valid as such, but it is admittedly difficult to determine the ancestral spiracle complement of the Hexapoda. Spermatological similarities between Collembola and Protura questionably comprise apomorphies (Jamieson 1987).

Order PROTURA

Principal autapomorphies include lack of tentorium, visual organs and antennae. Fore legs enlarged, usually carried lifted and anteriorly directed, richly furnished with

sensilla. Abdominal free limbs minute, their occurrence restricted to 3 anteriormost segments.

Order COLLEMBOLA

Principal groundplan autapomorphies include small number (6) of abdominal segments and specialised appendages on abdominal segments 1 (ventral tube), 3 (retinaculum) and 4 (furca). Thoracic legs with long penultimate segment presumably representing a composite tibiotarsus. Spiracles cervical or absent.

The unique abdominal segmentation confers upon the Collembola an extreme phenetic isolation within the hexapod, and indeed ateloceratan assemblage. It is possible, but of course conjectural, that ancestral Collembola were highly anamorphic and that lack of postembryonic segment addition is an autapomorphy (Boudreaux 1979). The total egg cleavage seen in Collembola is similarly unique among hexapods. As in totally cleaving myriapod eggs a typical blastoderm is eventually formed, however, and the collembolan cleavage mode may well be another apomorphy after all. Manton (1972, 1977) emphasised the uniqueness of the trunk design and related it to the hydrostatic jumping mechanism as known in detail in a tomoderid spring-tail; possibly, this character complex will prove autapomorphic for the order as a whole.

Class and Order DIPLURA (= Entognatha in Chapter 6)

Head with neither tentorium (François 1971) nor ocelli (absence of compound eyes in extant families apparently not resulting from a single loss event). Thoracic legs, according to Manton (1972, 1977) with unique development of trochanteral femur-twisting muscles and a similarly unique pivot at femur-tibia (or, perhaps, femur-patellotibia) joint. The monophyly of this order, including both the campodeid-like and the japygid-like Hexapoda, is not immediately obvious, but seemingly justified by the unique leg features noted by Manton in both lineages.

THE TRUE INSECTS, CLASS INSECTA

The monophyly of Archaeognatha + Thysanura *s.str.* + Pterygota seems very well founded and is widely agreed upon. Among the principal synapomorphies of the groundplans of its constituent taxa could be cited the structure of the antenna with its lack of muscles beyond the scape (first segment) and the presence of a large group of chordotonal organs ('Johnston's organ') in the pedicel (second segment). The posterior tentorium is developed, forming a transverse bar. The coxae of the thoracic legs primitively have no articulation with the sternum; the tarsi are subsegmented, and the pretarsal claws articulate on the distal tarsomere instead of on the pretarsal base (Boudreaux 1979). Females have an ovipositor formed by gonapophyses (limb-base endites) on segments 8 and 9. A long, annulated 'terminal filament' is developed from dorsum 11 (plus telson?). The spermatozoon has 1-3 'accessory bodies', developed from the centriole adjunct (Jamieson 1987). During early embryogenesis the germ band comes to be located within an amniotic cavity.

A characteristic complement of spiracles (one segmental pair from mesothorax to abdominal segment 8) may be ascribed to the insect groundplan (though abdominal spiracle 1 is absent in the Archaeognatha); a segment 8 spiracle does not occur elsewhere in hexapods, but it could be plesiomorphic.

The Archaeognatha and Thysanura *s.str.* are the primitively apterous insects and they have formerly been united in the taxon 'Thysanura'. However, there are good reasons for considering the Thysanura *s.str.* to be the cladistically closest relatives of the Pterygota, and these two groups are therefore now united in the subclass Dicondylia.

Subclass and Order ARCHAEOGNATHA

Compound eyes enlarged, medially contiguous. Spiracles 1 absent. The two aforementioned traits establish the monophyly of this small order. Moreover, it seems likely that the jump-facilitating specialisations in abdominal, skeletomuscular structure described from various machilid genera (Manton 1972, 1977; Bitsch 1973; Birket-Smith 1974) will prove to be characteristic for the entire order. It is difficult to assess which of the order's other peculiarities (such as the bilobed glossae and paraglossae) are actually apomorphies.

Subclass DICONDYLIA

Mandible with secondary (anterior) articulation acquired in addition to the primary posterior one; in the new articulation a cranial process fits a mandibular cavity (see, however, the remarks below concerning ephemeropteran mandibles). Primitive, ligamentous, endoskeletal plates accommodating mandibular and maxillary adductors absent; muscles in question have shifted origin to the cuticular pretentorium. Maxillary palp reduced in size, distinctly smaller than thoracic legs. Endoskeletal rods (fulcrum or fulturae) from hypopharynx suppressed. Postoccipital ridge complete. Gonangulum in ovipositor base fully developed, having an attachment to the first gonocoxa/gonapophysis in addition to the original articulations with T9 and gonocoxa 9 (see Bitsch 1974 for a discussion of gonangulum structure in primitively apterous insects). Abdominal tracheal system with segmental commissures and intersegmental connectives.

As noted below, the restructuring of the head endoskeleton may not be characteristic of the Dicondylia as a whole. On the other hand some further putative, dicondylan autapomorphies may prove valid. The basic tarsomere number (including 'basitarsus') of the thoracic legs is probably five (if the five-segmented condition in *Tricholepidion* is not autapomorphic, as believed by some). The mature sperm axoneme has the outer 'singlets' regularly distributed and not arranged in two groups as in the Diplura-Campodeidae and Archaeognatha, but it may be that the latter condition is derived (and evolved as parallelisms in the two groups in question). Baccetti (1979) considered the presence of crystalline protein (crystallomitin) in the sperm mitochondrial derivative to be another synapomorphy of the Thysanura *s.str.* and Pterygota; however, the Odonata lack crystallomitin, and

the Ephemeroptera are aberrant in having crystalline rods separate from the mitochondrial derivative (review by Jamieson 1987), so the actual groundplan condition in the Dicondylia remains questionable. Temporary closure of the amniotic cavity during early embryogenesis could be another dicondylan autapomorphy. Such closure has been said (D. T. Anderson 1973) to occur already in the archaeognathan *Petrobius*, but according to Larink (1983) the cavity in this taxon remains 'wide-open'. Larink further shows that, contrary to earlier statements, the amniotic cavity of the thysanuran (*s.str.*) *Lepisma* is actually completely closed in early developmental stages, even though an open amniopore does occur later on. It could well be that the same is true for another thysanuran (*s.str.*), *Thermobia*, which has been found to have an open amniopore (Woodland 1957).

Infraclass and Order THYSANURA *s.str.* (= Zygentoma)

The monophyly of non-apterygote Dicondylia (families Lepidothrichidae, Nicoletiidae, Maindroniidae and Lepismatidae) is very uncertain. The western Nearctic *Tricholepidion gertschi*, sole extant member of the family Lepidothrichidae, has retained a number of apparently primitive traits (including large abdominal sterna with posteriorly attached coxopodites, large number of pregenital styles and eversible sacs) not found in other thysanurans (*s.str.*), let alone pterygotes. According to Boudreaux (1979) *Tricholepidion* also has retained the cephalic, ligamentous endoskeleton. It is possible, therefore, that *Tricholepidion* is the sister group of all other Dicondylia and should be given ordinal rank. On the other hand, *Tricholepidion* and the Nicoletiidae share a probably apomorphic type of sensilla on the terminal filament (Wygodzinsky 1961), while sperm conjugation occurs in both *Tricholepidion* and Lepismatidae (Wingstrand 1973, *contra* Wygodzinsky 1961). Wygodzinsky considered sperm conjugation a forerunner of 'spermatolophid' formation in Nicoletiidae. Barlet (1981) observed a number of differences between the thoracic structure of Lepidothrichidae, Nicoletiidae and Lepismatidae; an extension of these comparisons to such pterygotes as primitive mayfly nymphs would undoubtedly prove rewarding.

Infraclass PTERYGOTA

Meso- and metathorax in mature stage(s) bearing wings with a venation and basal articulation that can apparently be derived from a single pattern (Kukalová-Peck 1983; Pfau 1986, similarly supports the monophyletic origin of the pterygote flight apparatus, but urges caution in the actual reconstructing of ancestral wing bases). Pleura of wing-bearing segments high and well sclerotised, stiffened by internal ridge from pleural wing process to coxal articulation. Pre- and metatentorium fused. Abdominal eversible sacs suppressed (although present on venter 1 in Grylloblattodea). Non-cuticular trunk endoskeleton absent (Boudreaux 1979).

There seems now to be wide agreement on the monophyly of the winged insects. The views of recent dis-

senters (La Greca 1980; Matsuda 1981) cannot be reconciled with modern systematic arguments (see Kukalová-Peck 1983; Riek and Kukalová-Peck 1984 and Pfau 1986 for a more detailed critique of Matsuda's views). The morphological basis for wing development continuously attracts much attention, and the 'wing-from-leg-base-exite' theory (Kukalová-Peck 1983, 1987 and Chapter 6; Birket-Smith 1984) now has considerable support, while the ecophysiological scenario of wing development remains conjectural (see Wootton 1986).

The Basic Pterygote Lineages

Only three of the basic pterygote lineages have survived to the present, viz. the Ephemeroptera, the Odonata and the Neoptera. It has been commonplace to unite all non-neopteran pterygotes, extinct and extant, in a taxon Palaeoptera, but there has been considerable uncertainty about whether this is monophyletic or not.

The venations of extant Ephemeroptera and Odonata are obviously different, but some Palaeozoic fossils assigned to the two lineages are phenetically very similar, and the formation of a basal wing brace through an anastomosis of the anterior anal vein with the posterior cubitus is considered a synapomorphy of the two (Kukalová-Peck 1985 and Chapter 6). This trait is illustrated for fossil taxa in Figs 6.14A, E, F and 6.15A–C. The anastomosis in modern dragonflies (Fig. 17.4) has been interpreted to lie at the lower end of the so-called 'anal crossing' (which, then should actually be CuP), whereas the anastomosis area in modern mayflies is secondarily desclerotised. According to Kukalová-Peck's wing interpretation, it is a synapomorphy of the ephemeropteran-odonate lineages plus the extinct Palaeoptera that the media always has a basal stem, while in some subgroups (and hence in the groundplan) of the Neoptera MA and MP are still separate at their bases. On the basis of these characters, some entomologists uphold the concept of a monophyletic taxon Palaeoptera.

On the other hand there is evidence from the fossil record (Kukalová-Peck 1983) that the shortened, bristle-like antennal flagella characteristic of modern mayflies and dragonflies cannot be ascribed to their last common ancestor. Moreover, while the aquatic lifestyle of ephemeropteran/odonatan immatures was previously considered to be derived, this is at least debatable now; primitiveness of aquatic immatures of ancestral pterygotes may well be acceptable to some who would be reluctant to go so far as to assume an aquatic origin of the tracheal system(s), as envisaged in the writings of Kukalová-Peck (see also Štys and Soldán 1980).

Evidence from extant representatives of the basic pterygote lineages provides some support for the alternative assumption of a sister-group relationship between the Odonata and the Neoptera (Kristensen 1975, 1981). Both are characterised by the absence of a moult in the imaginal (i.e. fully winged) stage, and, in spite of Boudreaux's (1979) *ad hoc* explanation of the ephemeropteran subimago as a secondary specialisation, it still seems very straightforward to consider it to represent an ancient condition. It must be noted, however, that the fossil record

allegedly indicates that moulting of flying stages has been independently eliminated within several pterygote lineages, including the Neoptera (Kukalová-Peck 1978 and Chapter 6). The tracheation of each wing and pterothoracic leg includes a component connected with the spiracle of the following segment; the absence of this component in the Ephemeroptera was considered a neotenic trait by Boudreaux (1979), but it deserves further attention. Occlusor muscles inserting directly on abdominal spiracular sclerites are present in some (but not all) Odonata (Miller 1962; Poonawalla 1966) and generally (and surely primitively) in the Neoptera, but they are lacking in Ephemeroptera, as in the primarily apterous insects. A more detailed reassessment of this odonatan/neopteran similarity is needed. According to Kukalová-Peck (1985 and Chapter 6) the anterior mandibular articulation is firm in the Odonata and Neoptera, whereas in Ephemeroptera, as in *Thysanura s.str.*, an ample articular membrane permits considerable freedom of movement. Whether this odonatan/neopteran similarity is indeed a parallelism seems an open question. Hypopharyngeal lobes in Odonata or Neoptera may never be true superlinguae (although at least in the case of some Plecoptera the issue remains debatable; Moulins 1971; Denis and Bitsch 1973), while these primitive formations, occurring in scattered groups of non-ptyergote hexapods, are prominent in the groundplan of nymphal Ephemeroptera. Similarly, a *long* terminal filament is retained in Ephemeroptera, but nowhere else in pterygotes; the homology (and hence plesiomorphy) of the posteromedian gill filament (Fig. 18.6) in nymphs of a few Plecoptera-Austroperlidae (Zwick 1980) remains questionable. Further loss characters shared by the Odonata and Neoptera include all tentoriomandibular muscle bundles except one, the tentoriolacinial muscle and probably some pterothoracic muscles. The absence of a common radial stem in some Ephemeroptera has been considered uniquely primitive in winged insects, but Riek and Kukalová-Peck (1984) attribute the same condition to the odonatan and palaeodictyopteroid lineages on the basis of evidence from fossils. The paired female gonopores in some female Ephemeroptera have similarly been considered uniquely primitive within pterygotes, but Boudreaux (1979) and Bitsch (1979) are probably correct in considering them a secondary feature. According to the latter view the primitive condition in the order is exhibited by those taxa that have a median vestibulum into whose anterior end the gonoducts open (recalling conditions in non-ptyergote insects).

It may be added that the monophyly of Odonata-plus-Neoptera has very recently gained support from a study of ribosomal DNA (Wheeler 1989).

If the evidence for the monophyly of both the Odonata plus Ephemeroptera and the Odonata plus Neoptera is inconclusive, the same is certainly also true of the putative ephemeropteran/neopteran synapomorphies suggested by Boudreaux (1979) and discussed by Kristensen (1981). Perhaps the strongest argument (already pointed out by Brinck 1962) concerns sperm transfer, which in the Odonata is still, in a sense, 'indirect'; the gonopore-to-

gonopore mode could thus be conceived as a shared derived character of Ephemeroptera and Neoptera.

The conclusion seems inescapable that even though the 'monophyletic Palaeoptera' model is now preferred by Kukalová-Peck and other palaeontologists, the problem of the basic dichotomy in extant pterygotes cannot be solved without postulating disturbing homoplasy one way or another.

Division and Order EPHEMEROPTERA

Adults with non-functional, strongly reduced mouthparts. Antennal flagellum small, bristle-like (parallelism with Odonata). Fore wing with basal 'subcostal brace' formed by anastomosis of strongly arched putative ScA with ScP, hind wings markedly smaller than fore wings. Male fore legs markedly elongate, adapted for seizure of females during mating flight. Sperm axoneme without central tubules. The paired phallic organs of most male mayflies may indeed be genuinely primitive, but then independent modifications of the copulatory apparatus must have taken place repeatedly in primitively apterous insects. Ordinal autapomorphies of mayfly nymphs are not obvious. The mandibular articulation presents intriguing problems. Most examined taxa have three points of articulation: anterior, middle and posterior, but the middle (lateral) one is lacking in the siphonurid examined by Schönmann (1981); since the Siphonuridae are considered a primitive grade, paraphyletic in terms of other mayflies (McCafferty and Edmunds 1979), one might *a priori* consider the middle articulation a secondary trait evolved within the order. As noted by Schönmann it is the middle articulation of the 'typical' mayfly mandible that would seem to correspond in position to the anterior condyle of commonplace dicondylous mandibles, but its structure does not support the homology; it is a thickening in the mandibular base that fits a concavity in the cranial margin, while normally the reverse is true. The mandibular component of the anterior articulation of the mayfly mandible is a groove (described as a 'slider' by Kukalová-Peck 1985 or 'sliding articulation' in Chapter 6), but it fits the *medial* margin of the base of the anterior tentorial arm (Schönmann 1981); in the Thysanura *s.str.* the anterior cranial condyle is situated laterad of the tentorial base (Chaudonneret 1950) and this is generally true of non-ephemeropteran pterygotes also. Conditions in the Ephemeroptera thus appear to be autapomorphic.

Division and Order ODONATA

Dragonfly autapomorphies are prominent. Adult prelabium/palp complex modified. Antennal flagellum short, bristle-like (parallelism with Ephemeroptera). Pterothoracic segments with strong backwards slant, terga small; mesepisterna almost meeting mid-dorsally in front of wings; flight apparatus (described in detail by Pfau 1986) unique. Secondary copulatory organ on male venter 2–3. Nymphs aquatic, with complexly modified labium forming prehensile 'mask'.

The wing venation of extant dragonflies has been notoriously difficult to interpret. According to Riek and Kukalová-Peck (1984) a kink in CuP at the site of fusion

with AA is an apomorphic feature that can be traced back to the earliest fossil representatives of the odonatan lineage.

Division NEOPTERA

Wing base with characteristic complement of axillary sclerites and fold-lines (Wootton 1979); of special note is the '3rd axillary sclerite' which accommodates the insertion of the pleural wing folding muscle, and rotates when the wing is folded backwards over the body. Vein R never forked from base. Ovipositor (when retained) with 3rd valvulae developed in full length, ensheathing 1st and 2nd valvulae, or actually integrated in ovipositor shaft. There is some indication that the trochantin in the neopteran leg base is another neoformation (Boudreaux 1979; Kukalová-Peck 1983 and Chapter 6). The weak wing-fluting is considered primitive by Kukalová-Peck.

The Basic Neopteran Lineages

Twenty-five extant orders of neopteran insects are recognised in this book (Fig. 5.5), although three of these (Blattodea, Isoptera and Mantodea) are often combined into a single order (Dictyoptera) and another (Psocoptera) may be paraphyletic (see below). Eleven of these are grouped into the taxon Endopterygota (= Holometabola) and another four into the taxon Paraneoptera; the remaining ten orders are here classified as Neoptera *incertae sedis*. Derived character states have a markedly reticulate distribution among the latter orders, so their relationships to each other and to the Endopterygota and Paraneoptera remain unclarified; overall they are primitive insects and may conveniently be treated collectively as 'the lower Neoptera'. Minet and Bourgoin have recently (1986) suggested that tarsal 'plantulae' are a genuine synapomorphy of all the lower neopteran orders (the Zoraptera would represent a secondarily simplified state), which could therefore be united in a monophyletic taxon 'Polyneoptera', as already envisaged by Martynov (1925); this interesting proposal deserves further attention and documentation. One of the orders, the Plecoptera, has aquatic immatures and some structural details (see below) that may be uniquely primitive at the neopteran level; it is possible that they are the sister group of all other Neoptera. An enlarged hind wing anal area ('vannus') is shared by the 'orthopteroid' orders Orthoptera, Phasmatodea, Dermaptera and Dictyoptera and it could well be a genuine synapomorphy. However, the Plecoptera have a similarly enlarged vannus, so either it has been independently evolved at least twice among lower Neoptera, or the Plecoptera do belong to a monophyletic 'orthopteroid' assemblage. In the latter case the plesiomorphies retained only by the Plecoptera must have been lost independently on other occasions within the Neoptera.

Order PLECOPTERA

Ordinal autapomorphies not obvious. Tarsi 3-segmented. Males without 'gonostyli' and phallic organs on abdominal segment 9. Females without genuine ovipositor (but secondary substitutes occasionally present, Zwick 1980). Gonads in both sexes anteriorly united. Nymphs aquatic,

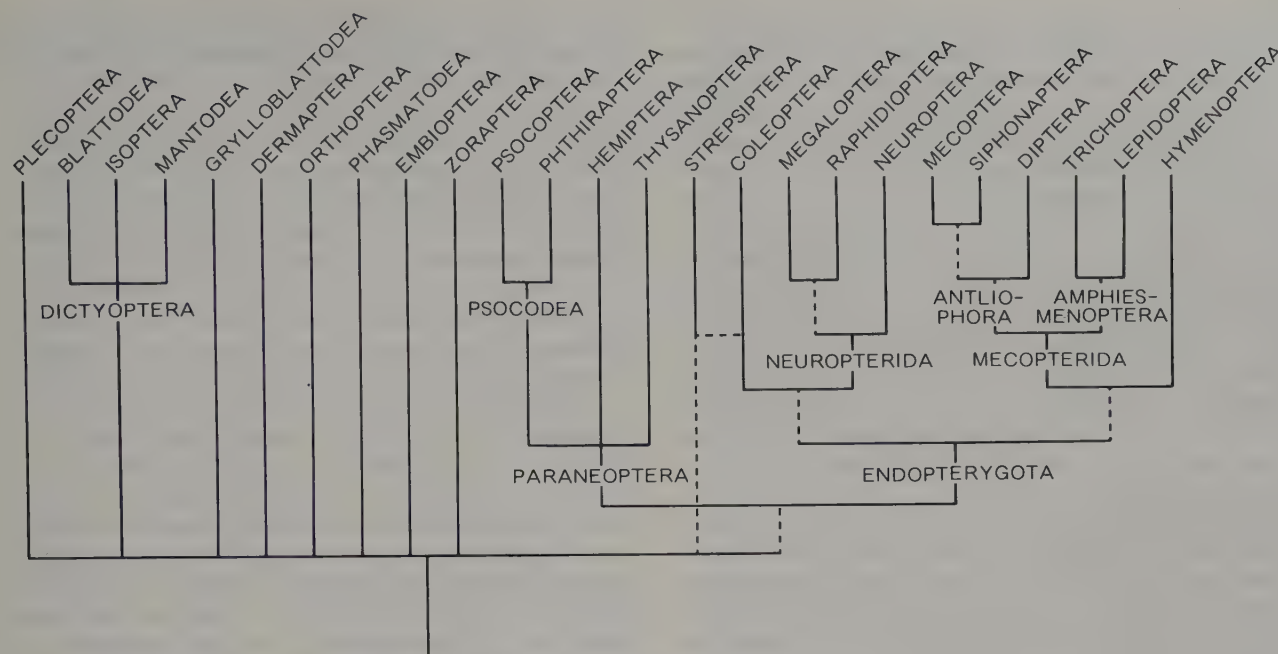


Fig. 5.5 Proposed phylogeny of Pterygota-Neoptera. Stippled lines indicate groupings that are considered doubtfully monophyletic.

with allegedly unique ventrolongitudinal musculature (Zwick 1980).

The possible implications of the enlarged hind wing vannus are mentioned above. Absence of segment 9 phallic organs is shared with the Embioptera, and the tarsomere reduction and lack of male 'gonostyli' and functional ovipositor is shared with the Embioptera, Dermaptera and Zoraptera (with only two tarsomeres) among lower Neoptera. A noteworthy plecopteran/embiopteran similarity is the presence of midventral excurrent ostia in the dorsal vessel in the metathorax; the Embioptera actually have such ostia also in the mesothorax and in abdominal segment 1 (Nutting 1951). Since midventral ostia have been reported from abdominal segments 1–5 in Thysanura, a series of such ostia from the mesothorax to 5 has been tentatively ascribed to the insect groundplan (Kristensen 1975); however, this is necessarily conjectural, and the thoracic ostia could indeed be plecopteran/embiopteran synapomorphies.

Plecopteran traits that may be uniquely primitive at the neopteran level include a transverse stipital muscle, metameric outlet ducts in the testis (Zwick 1981c) and, questionably, the retention of a terminal filament in a few nymphs. Paired male gonopores also occur in the Dermaptera, and neither Baccetti (1979) nor Jamieson (1987) have attached phylogenetic weight to the allegedly primitive spermatological characters known from the Plecoptera. As noted above, it is debatable whether hypopharyngeal lobes present in some stoneflies are true superlinguae.

Orders BLATTODEA, ISOPTERA and MANTODEA (= DICTYOPTERA)

Three phenetically distinctive taxa are included here: the Mantodea, the Blattodea and the Isoptera. Principal

synapomorphies include the 'perforate' tentorium (processes on the anterior arms fuse medially in front of the oesophageal nerve connectives) and the female genitalia with a shortened (but primitively still quite complete) ovipositor hidden above a large subgenital plate formed by S7. Sclerotised crop armature distinctive (Judd 1948).

The three constitutive taxa of the Dictyoptera are often each given ordinal rank, and they are treated as distinct entities later in the present work. It remains an open question, however, whether the cockroaches are actually paraphyletic in terms of the termites; the idea (see Hennig 1981) that the apterous Northern Hemisphere cockroach genus *Cryptocercus* is the cladistically closest relative of the termites has received new support from a recent study of its behaviour and gland equipment (Seelinger and Seelinger 1983). The distribution of segmental arteries in Dictyoptera is intriguing. Such formations are present from the mesothorax to abdominal segment 4 in cockroaches (including *Cryptocercus*), in segments 1–4 in some (not all) mantids, but not in termites, or indeed in other lower Neoptera (Nutting 1951); they might indicate a sister-group relationship between cockroaches and mantids (Boudreaux 1979), but alternatively could be secondarily reduced in the termites (Kristensen 1975), where regressive traits abound.

Order GRYLLOBLATTODEA

The smallest and most homogeneous insect order, restricted to the temperate Holarctic. Head prognathous, with compound eyes more or less regressed (ommatidia not contiguous) and ocelli lacking. Wings absent. Hind coxae large, conical. Metathoracic spina present, probably a neof ormation (corresponding spina present nowhere else in the Recent Insecta). Dorsal vessel (Nutting 1951) with paired, segmental excurrent ostia opening into dorsal

diaphragm chambers filled with phagocytic tissue. Venter 1 with median eversible sac, probably a neoformation (eversible sacs are not present on 1 in Recent primitively apterous insects, but have been identified by Kukalová-Peck in Palaeozoic members of that grade). Male gonopods and phallomeres asymmetrical.

The chambers around the excurrent heart ostia are shared only with some Orthoptera-Ensifera and would seem to support a sister-group relationship between the Grylloblattodea and the Orthoptera, but the chambers must, then, have been lost independently on several occasions within the latter. The Ensifera-like ovipositor is very probably plesiomorphic at the lower neopteran level (Kristensen 1975). The notopteran coxal shape has been considered evidence for a close relationship with the Dictyoptera, but this is uncertain (Kristensen 1975).

Order DERMAPTERA

Strongly autapomorphic. Head prognathous, but without genuine gula. Ocelli absent. Fore wings (when retained) short elytra, with venation at most faintly indicated. Hind wings (when retained) with remigium much reduced, melanised; large vannus complexly folded in repose. Male without 'gonostyli' on 9. Female with subgenital plate formed by enlarged S7; ovipositor vestigial (when at all retained), with only 2 valve pairs. Cerci of adults forcipate, without discernible segmentation (exceptions in possibly neotenic ectoparasites). Sperm axoneme with 2 dense sheaths, surrounding outer and inner singlets respectively.

Apomorphies indicating possible links with Plecoptera and Embioptera are discussed under those orders. The enlarged female S7 would support a sister-group relationship to the Dictyoptera, while the sperm specialisation is shared with the Phasmatodea and thus would support a sister-group relationship to that order (Jamieson 1987). The ectoparasitic Hemimerina are now considered the sister group of all other earwigs, while the similarly ectoparasitic Arixeniina may be subordinate within the Labioidea (Popham 1985).

Order ORTHOPTERA

Included here are the Ensifera and the Caelifera, for which Kevan (1986) uses the names Grylloptera and Orthoptera *s.str.*, respectively; it is widely believed that these constitute together a monophyletic entity, and a small suite of putative synapomorphies supports this notion: 1) lateral flange of pronotum largely covering pleuron, which correspondingly becomes largely desclerotised (cryptopleuron); 2) hind leg modified for jumping by straightening of femur/patello-tibia joint; 3) femur enlarged to accommodate large tibia extensor muscle; 4) hind tibia with 2 dorsal teeth rows (Minet and Bourgoin 1986); 5) first thoracic spiracle horizontally divided; 6) wing pads of late nymphal instars twisted.

It is a further, derived similarity between Ensifera and Caelifera that the ovipositor base is hidden by an enlarged subgenital plate which apparently pertains to venter 8. In the Caelifera this is actually formed ontogenetically by simple enlargement of S8. In the Ensifera, however, the

plate is formed by outgrowths from the ventral 7/8 inter-segmental membrane taking the place of the original S8, which becomes extensively desclerotised during ontogenesis.

It has been stressed repeatedly by Kevan that the Ensifera and Caelifera are phenetically different to the point where ordinal status for each seems warranted. But, whereas the monophyly of the Caelifera seems unquestionable (supported, e.g. by their uniquely derived ovipositor), the monophyly of the Ensifera is less certain, although their proventricular armature and the male accessory gland complex would seem to support it (Kristensen 1975).

A sister-group relationship between the Caelifera and Phasmatodea, suggested by Sharov (1968), is inconclusively supported. Derived similarities include the enlarged arolium (questionably a caeliferan groundplan trait), simple crop intima (possibly plesiomorphic) and a true S8 subgenital plate in females. The above-mentioned evidence for the monophyly of Ensifera + Caelifera would surely appear more weighty. For a possible association of the Grylloblattodea with the Orthoptera see above.

Order PHASMATODEA

Groundplan autapomorphies not very prominent (Kristensen 1975). Paraglossa with additional, dorsal, flexor muscle. Prothorax with repellent gland opening near anterior notal corner. Pretarsal arolium enlarged. Male without 'gonostyli' on 9. Female with subgenital plate ('operculum') formed by enlarged S8; ovipositor short. Cerci unsegmented. Mesenteron posteriorly with pyriform, filament-bearing processes. Spermatozoon without mitochondria; axoneme with two dense sheaths, surrounding outer and inner singlets respectively. Eggs thick shelled, with operculum.

Arguments for relating the stick-insects to the Embioptera, the Dermaptera or the Orthoptera (and more specifically to the Caelifera) are discussed under those orders.

Order EMBIOPTERA

Strongly autapomorphic. Head prognathous, with true gula. Ocelli absent. Paraglossa with additional, dorsal, flexor muscle. Basal segment of fore tarsus greatly swollen, containing silk gland; silk used for spinning tubular galleries. Hind femora enlarged. Females always apterous. Male wings, when retained, with simplified venation and (primarily or secondarily?) without enlarged vannus. Males without 'gonostyli' and phallic organs on abdominal segment 9. Females without ovipositor. Cerci 2-segmented. Maternal brood care present.

Similarities with the Plecoptera are noted earlier. Derived characters shared with the Dermaptera include, besides the genitalia regressions, the maternal brood care and a prognathous head without ocelli. An embiopteran/dermapteran sister-group relationship might seem an attractive hypothesis, but prognathism in earwigs has a different morphological basis. The aberrant, dorsal paraglossa flexor would seem to indicate a sister-group rela-

tionship with the Phasmatodea (Rähle 1970, see Kristensen 1975) while, as recently noted by Minet and Bourgoin (1986), a sister-group relationship with the Zoraptera could be proposed on the basis of the strongly developed hind femora (correlated with a similarly strong development of the tibia depressor) and supported by their gregarious habits, as well as the small tarsomere number and genitalia regression.

Order ZORAPTERA

Small size. Tarsi 2-segmented. Wings (when present) with simple venation; hind wings distinctly smaller than fore wings. Female postabdomen with subgenital plate on venter 8; ovipositor vestigial. Only 6 Malpighian tubules. Only 2 abdominal ganglia.

This small order of minute insects is morphologically very little known. The small number of tarsomeres, Malpighian tubules and abdominal ganglia have been considered indicative of a sister-group relationship to orders here included in the Paraneoptera. Admittedly, the zorapterans, with their seemingly overall simplified structure, could have their closest relatives among the lower neopterans as well; however, a previously suggested specific link to the termites appears untenable (Kristensen 1975). The above mentioned recent proposal of a sister-group relationship to the Embioptera (Minet and Bourgoin 1986) deserves further attention.

Subdivision PARANEOPTERA (= ACERCARIA, HEMIPTEROID ASSEMBLAGE)

Maxillary lacinia slender and elongate, detached from stipes. Postclypeus (called frons by Matsuda 1965 and Hamilton 1981) enlarged, accommodating similarly enlarged cibarial dilator(s). Tarsomeres 3 (or less). Female with gonangulum fused to T9. Cerci absent (at least in Recent forms). At most 6 Malpighian tubules. Only one abdominal ganglionic mass. Sperm acrosome bilayered; perforatorium lost (Jamieson 1987).

The synapomorphies of the three extant 'hemipteroid' orders included here, Psocodea, Thysanoptera and Hemiptera, may not appear to be 'strong' ones, but the monophyly of the composite group is widely accepted, and indeed there seems to be no evidence for relationships of any of the orders to other neopterans.

The absence of a discrete S1 must now be discarded as a further paraneopteran autapomorphy since it is retained in some true bugs (N. M. Andersen 1982; Štys 1985), even though Andersen interprets its occasional considerable size in gerrids as a secondary trait.

Striking specialisations of the spermatozoon (two flagella, only one mitochondrion per axoneme, axoneme inserted at acrosome base) have been found in the Thysanoptera as well as the parasitic section of the Psocodea (the axoneme-insertion character is lacking in the sucking lice), while biflagellarity alone has been found in some, but not all, of the Hemiptera-Heteroptera and non-parasitic Psocodea (Psocoptera) examined (Baccetti 1979; Jamieson 1987). It is perhaps most straightforward to attribute biflagellarity to the paraneopteran groundplan, and hence interpret uniflagellarity in

this lineage as a secondary character reversal; alternatively biflagellarity could be considered an 'underlying synapomorphy' (see Saether 1979) at the paraneopteran level. The other spermatological characters indicate a sister-group relationship between the Thysanoptera and the Psocodea. Since the monophyly of the latter is well founded (and since a sister-group relationship between the Thysanoptera and the parasitic lice hardly appears to be ecologically plausible) an *ad hoc* explanation of the absence of these sperm specialisations in the non-parasitic 'Psocoptera' as secondary would be needed. To the spermatological evidence for a sister-group relationship between the Psocodea and the Thysanoptera may be added the similar arrangement of the large dorsal cibarial pump muscle with its median tendon. On the other hand this must be weighed against the evidence for the widely accepted monophyly of a superorder Condylgnatha comprising the Thysanoptera and Hemiptera. This evidence is primarily related to mouth-part structure, in that the Thysanoptera piercing apparatus is considered an early offshoot of the transformation line leading to the hemipteran configuration (Hamilton 1981); the dorsal shift of the anterior tentorial pits, the narrowed labrum, the unicondylar mandibular stylets and the lacinial stylets (probably not much altered from the paraneopteran ground plan), as well as expanded hypopharyngeal apodemes, would be shared derived features. Heming (1980) believed that the mandibles might not have been much modified for piercing in the last common ancestor of Hemiptera and Thysanoptera. The cautious solution of representing paraneopteran interordinal relationships as an unresolved trichotomy may be preferable at present.

The affinities of the Paraneoptera remain uncertain. It is just possible that they are the sister group of the Endopterygota with which they share characteristics in ribosomal DNA (Wheeler 1989), a sclerotisation on the jugum (Hamilton 1972c), perhaps pterothoracic endosterny (widened sterna would then be secondary), gonopod morphogenesis (Boudreaux 1979, but note that acceptance of this similarity does not necessarily entail acceptance of the Boudreaux view that the neopteran/endopterygote gonopod is itself a neoformation). Absence of ocelli in immatures cannot be upheld as a specialisation common to Paraneoptera and Endopterygota.

Orders PSOCOPTERA and PHTHIRAPTERA (= PSOCODEA)

Preoral cavity with specialised water-vapour uptake apparatus (see Rudolph and Knülle 1982) comprising cibarial pump and unique hypopharyngeal sclerotisations ('lingual sclerites' and 'filamentous ducts'). Antennal flagellum basally with rupture-facilitating cuticle modifications. Cardo obliterated as a discrete sclerite. Lateral hypopharyngeal arm absent. Ovipositor simplified; valvulae not interlocked.

The ovarioles are polytrophic in the Psocodea and nowhere else among the non-endopterygote insects; this might be another psocodean autapomorphy. However, since the telotrophic ovarioles of Hemiptera are presumably derived from the polytrophic type (Heming 1977), it may be equally parsimonious to attribute the latter to the

paraneopteran ground plan and interpret the panoistic ovarioles of Thysanoptera as a character reversal. Recent studies on thysanopteran ovariole structure (Pritsch and Büning 1989) lend support to the last suggestion. Further putative psocodean autapomorphies are discussed by Lyal (1985a).

The interrelationships within the Psocodea have been subject to considerable discussion during the last decade (Lyal 1985a). The monophyly of a taxon Phthiraptera comprising the parasitic lice is very well founded, while the suggestion by Kim and Ludwig (1982), that the chewing lice ('Mallophaga'), are monophyletic is rejected. Lyal rejects previously proposed putative autapomorphies (primarily in egg and embryo characters) of an entity consisting of the non-parasitic Psocodea ('Psocoptera') and tentatively suggests that the 'Psocoptera'-Liposcelidae are the closest relatives of the Phthiraptera. The 'Psocoptera' are treated as a separate entity in this work, but the notion that this group is paraphyletic in terms of the parasitic lice seems to make very good sense from an evolutionary-ecological point of view.

Order THYSANOPTERA

Highly autapomorphic. Principal specialisations include asymmetrical mouth cone, piercing left mandibular stylet (right mandible lost) and lacinial stylets. Pretarsus with eversible vesicle (adhesive arolium, see p. 510); claws reduced in adult. Wings, when present, almost linear, with very long marginal setae. Ovarioles panoistic. Sperm characteristics discussed above. Last immature instars inactive, with considerable internal reorganisation.

Order HEMIPTERA

Primarily characterised by unique sucking mouth apparatus, distally comprising mandibular and coadapted maxillary stylets lodged in transversely segmented labial rostrum; maxillary stylets enclosing alimentary and salivary canals between them; palps absent. Ovarioles telotrophic.

The Hemiptera are by far the largest order of non-endopterygote insects, and in terms of morphological diversity they are perhaps surpassed only by the Diptera. The monophyly of a taxon 'Homoptera' constituted by the Hemiptera less the Heteroptera (or Heteroptera + Coleorrhyncha) remains debatable, and this taxon is not recognised later in this work; the diagnostic homopteran trait mentioned by Hamilton (1981), viz., the distinctive loral sutures, is questionably apomorphic. In any case, this uncertainty as well as the phenetic heterogeneity of the 'Homoptera' strongly speak against a separation at the ordinal level.

Subdivision ENDOPTERYGOTA (= HOLOMETABOLA)

Immature post-ovum instars, except last, are 'larvae' which differ markedly from the adult. True ocelli absent in immatures; number of eye units (probably primitively contiguous ommatidia, usually isolated stemmata) not increasing during larval life; larval eyes disintegrating and adult compound eyes and ocelli formed *de novo* during last immature instar (Paulus 1986). Rudiments of

wings and genital appendages develop in cavities below the body wall, only becoming external through evagination at penultimate moult. Last immature instar, the 'pupa', practically always (and most probably primitively in extant endopterygotes) inactive and non-feeding (while the pharate adult may be quite agile). Ovarioles probably primitively polytrophic (reversal to panoistic type occurring within the Neuropterida and Mecopterida-Antliophora, King and Büning 1985).

Birket-Smith (1984) contended that the thoracic legs of larval endopterygotes are not homologous with those of the adults, but represent a more medial series of segmental appendages, to which the abdominal prolegs pertain as well. On the other hand the thoracic legs of non-endopterygote insects are homologous throughout all stages. The reasons given for this radical reinterpretation of endopterygote larval legs do not appear compelling, and the thoracic legs of endopterygote larvae are not here considered basically different from their counterparts in non-endopterygotes.

Apart from 'the Strepsiptera problem' the monophyly of the Endopterygota would appear to be uncontroversial and generally accepted as such, but operational autapomorphies of adult Endopterygota still remain to be worked out. The endopterygote mode of metamorphosis permits larvae and adults to diversify independently. This has promoted the success of the group to the extent that today more than eighty percent of hexapod species are endopterygotes.

The extant Endopterygota may tentatively be classified into a neuroptero-coleopteroid group and a hymenoptero-mecopteroid group. The affinities of the Strepsiptera remain enigmatic.

Order STREPSIPTERA

Highly autapomorphic, sexual dimorphism extreme. Adults non-feeding. Tentorium absent. Male antennae with conspicuous process on some flagellar segments. Imaginal eyes 'stemmataran faceted eyes' (Paulus 1979). Males with fore wings transformed into halteres; hind wings very broad, fan-like, vannal component of fan only small; venation simple, without cross-veins. Mesothorax much smaller than metathorax, metapostnotum + part of abdominal dorsum 1 forming a prominent, posteriorly tapering plate. Male gonopods absent. Female apterous, primitively with homonomous trunk segments, without external genitalia. Ovaries diffuse. Second and later (but primitively not last) larval instars endoparasitic in some other insect.

The Strepsiptera are commonly associated with the Coleoptera because of their posteromotorism (flight using metathoracic wings only) and this sister-group relationship remains a real possibility. The suggestion that the Strepsiptera are actually a subordinate entity within the polyphagous beetles cannot well be reconciled with the apparent persistence of a tegula and a few true veins in the haltere, or with the retention of a discrete tarsus and paired claws in the free last-instar larva of mengenillid Strepsiptera.

The pupal stage of (at least some) Strepsiptera is pre-

ceded by a couple of pharate instars with external wing buds. This would seem to make the assignment of this order to the Endopterygota questionable. If the eyes of adult Strepsiptera are indeed larval eyes carried over, this would also speak against this assignment. The conventional view of placing the Strepsiptera adjacent to the beetles is adopted in the present work, but a tentative placing of these strangely aberrant insects as *Neoptera incertae sedis* might be preferable at present.

Informal Group NEUROPTERIDA + COLEOPTERA

Cruciate cervical muscles absent. Female terminalia (Fig. 5.6) with 1st valvulae (gonapophyses 8) fused and shortened, 2nd valvulae (gonapophyses 9) lost as discrete formations, 3rd valvulae (gonostyle 9) sensory, gonangulum fused with T9, cerci reduced, not articulated. Telotrophic ovarioles occur in most Megaloptera/Raphidioptera and in Coleoptera-Polyphaga; however the polytrophic condition occurs in some beetles and neuropterans, while panoistic ovarioles occur in some Megaloptera and Neuroptera (King and Büning 1985). Previous assumptions of a Coleoptera/Neuropterida synapomorphy in larval stemma structure have been discarded, since recent investigations have led to revised models for the groundplans in the two taxa (Paulus 1986).

Although the monophyly of this order-group is not supported by conspicuous autapomorphies it has been in vogue for many years; very recently it has gained addi-

tional support from ribosomal DNA data (Wheeler 1989). Boudreaux (1979, 1981) held different views, assuming the Coleoptera to be the sister-group of the rest of the Endopterygota, and the Neuropterida to be the sister-group of the Mecopterida. The evidence for these assumptions was questioned by Kristensen (1981). The absence of gastric caeca may perhaps be upheld as a possible synapomorphy of non-coleopteran endopterygotes, but the transverse division of their male gonopod is not here considered apomorphic (nor would its absence in the Coleoptera be agreed upon). The abdominal appendages of larval Megaloptera, Neuroptera-Sisyridae, Hymenoptera and Mecopterida (where they are diverse and of scattered occurrence) cannot well be conceived as stemming from a single 'derepression' event. Putative synapomorphies of the Neuropterida and the Mecopterida included pronounced cryptosterny (median invagination of the sternum) and well demarcated mera on the pterothoracic coxae; both traits may actually be endopterygotan groundplan attributes, and their absence secondary.

Section NEUROPTERIDA (= NEUROPTEROID ORDERS)

Ovipositor with 3rd valvulae fused and equipped with a series of short intrinsic muscles. Metapostnotum divided medially; T1 with caudally-bifid mediolongitudinal suture (Achtelig 1975, 1981; other putative neuropterid synapomorphies in the thoraco-abdominal transition region may

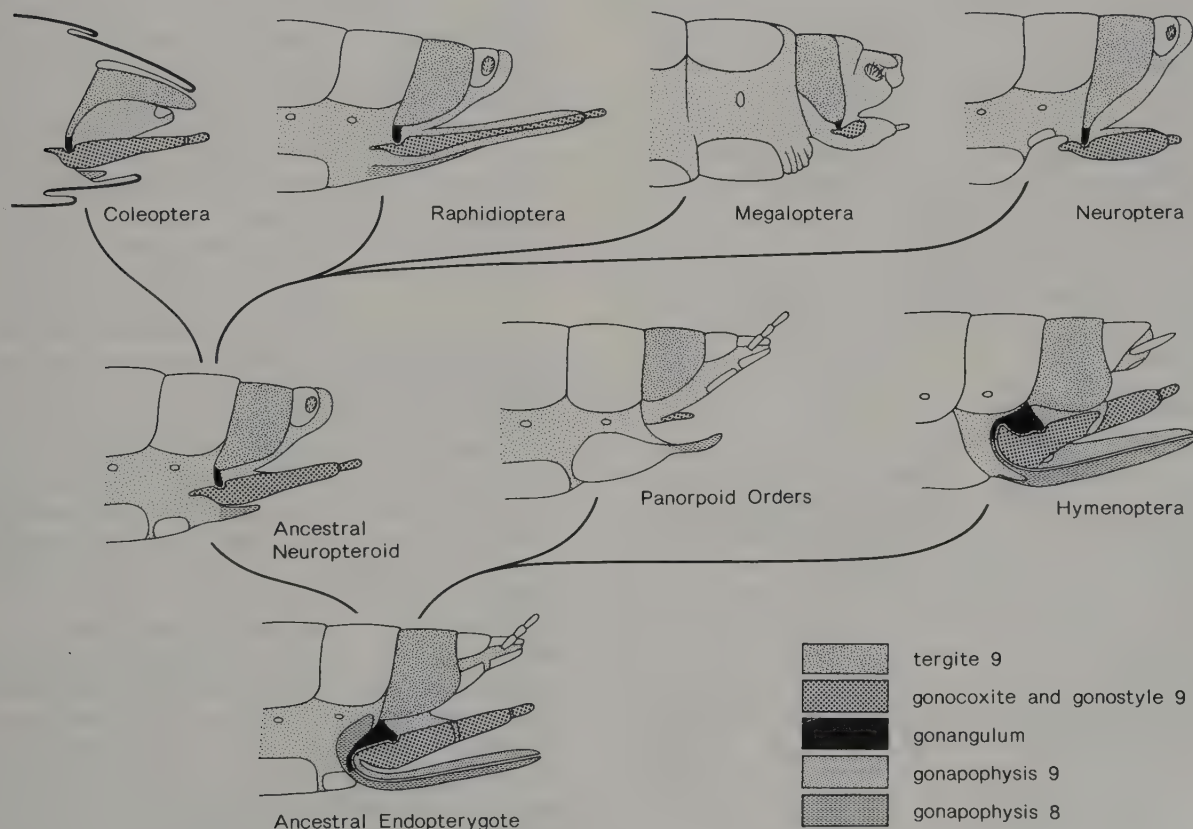


Fig. 5.6 Evolutionary pattern of Endopterygota as indicated by female terminalia.

[After Mickoleit 1973]

be of more questionable significance). Proventriculus with unpaired diverticulum.

The three orders included here, Megaloptera, Raphidioptera and Neuroptera are sometimes included in a single order. However, even if their monophyly is now well established, the synapomorphies are admittedly not prominent traits. Neuropterid larvae are consistently predacious. Within the section there is apparently a sister-group relationship between the Megaloptera + Raphidioptera and the Neuroptera. Possible synapomorphies (review by Achtelig 1981) include the presence of a gula (lacking, probably secondarily, in larval Megaloptera-Sialidae), firm connection of metepimeron to an apophysis-bearing 'postepimeron' pertaining to abdominal segment 1, specialised T2 with reinforced acrotergite accommodating origin of strong polyintersegmental muscle, telotrophic ovarioles with special nurse chambers (in Raphidioptera and some Megaloptera only), and a derived cleaning behaviour. Evidence for a sister-group relationship between the Megaloptera and the Raphidioptera + Neuroptera has been discussed by Achtelig and Kristensen (1973), while Boudreaux's (1979) suggestion of a sister-group relationship between the Raphidioptera and the Megaloptera + Neuroptera was briefly criticised by Kristensen (1981).

Order MEGALOPTERA

Imaginal autapomorphies have not been worked out in detail. Fore wing Sc towards apex anastomosing or fusing with R (as in numerous Neuroptera). Ovipositor shortened (as in numerous Neuroptera). Larva aquatic; stipes divided; abdominal segments 1-8 (or 7) with slender lateral gills.

There will not be general agreement with the view (forcefully advocated by Hinton 1955b) that the aquatic lifestyle and abdominal gills of juveniles are derived traits at the endopterygote level. But the notion that the Megaloptera have evolved from ancestors with terrestrial larvae devoid of abdominal appendages does not necessarily preclude the possibility that megalopteran gills actually represent an ancient morphological complex which has reappeared in consequence of a genetic reconstruction.

Order RAPHIDOPTERA

Autapomorphies of this very homogeneous, exclusively Northern Hemisphere order are not prominent. Marked posterior narrowing of the prognathous head capsule and elongation of the pronotum are not greatly different from conditions in Megaloptera-Corydalidae. Fore wing Sc runs into anterior wing margin, but may bend backwards (as a crossvein-like strut) and fuse with R. Imaginal tarsi with expanded (bilobed) third tarsomere, pretarsal arolium absent.

The long ovipositor of female snakeflies does not deviate much from that of the neuropterid groundplan (Mickoleit 1973).

Order NEUROPTERA

Monophyly demonstrated by weighty larval autapomor-

phies. Slender mandible and maxillary stylet (stipitolacinal) coadapted, enclosing a food canal between them. Mesenteron (mid gut) posteriorly closed; 'cryptonephridial' association of most Malpighian tubules with proctodaeum; Malpighian tubules produce silk for pupal cocoon. One of the seven ancestral stemmata vestigial (parallelism with Megaloptera; Paulus 1986).

Section and Order COLEOPTERA

Fore wings forming sclerotised elytra mostly with undiscernible venation, their hind margins contiguous in resting position, tegula absent. Hind wings alone responsible for flight propulsion, primitively longer than elytra, packed beneath elytra in repose, with much reduced vein branching in remigium. Abdominal terga weakly sclerotised; abdominal spiracles located in subelytral cavity. Head capsule usually (and probably primitively) closed ventrally by a gula. True labial glands primitively absent. Profurcal arm not fusing with pleuron (secondary condition?). Genital segments of both sexes retracted into preceding segments.

The groundplan of this overwhelmingly species-rich insect order is largely similar to that of the Neuropterida, but the wing modifications confer upon the beetles a most distinctive habitus and surely contributed much to their evolutionary success.

Informal Group HYMENOPTERA + MECOPTERIDA

The Hymenoptera on one hand are strikingly autapomorphic in their wing venation, and on the other do not exhibit any prominent similarities with other endopterygote assemblages; they thus appear as an isolated taxon. Their putative sister-group relationship to the Mecopterida is so far based only on the unpaired pretarsal claw in the larval leg and the silk secretion from larval labial glands. The 'eruciform' larval type itself is more doubtful in this context, since the lowest mecopteran larvae (Nannochoristidae) are quite prognathous and this is true also of the lowest Amphiesmenoptera (Kristensen 1984e).

Section MECOPTERIDA (= PANORPOID ORDERS)

Pleural muscle inserted on 1st axillary sclerite (Fig. 5.7A). Larval maxillary stipes (Fig. 5.7B) transversely divided (parallelism with conditions in Megaloptera and also Neuroptera, but in the latter the larval maxilla is overall profoundly modified; Rousset 1966); cranial extensor muscle of dististipes present in addition to commonplace flexor; cranial cardo promotor, stipitolacinal and stipitogaleal muscles absent. Larval labial palp muscles absent. Ovipositor vestigial or completely lost (Fig. 5.6).

The monophyly of the Mecopterida seems generally accepted, even though its autapomorphies are admittedly inconspicuous. The loss of the outer tergocoxal 'remotor' in the pterothorax was long considered another mecopterid autapomorphy. This muscle has now been recorded from a few primitive moths (Agathiphagidae, Lophocoronidae; Kristensen 1981 and unpubl.); should it be regarded as an autapomorphic character reversal in these cases?

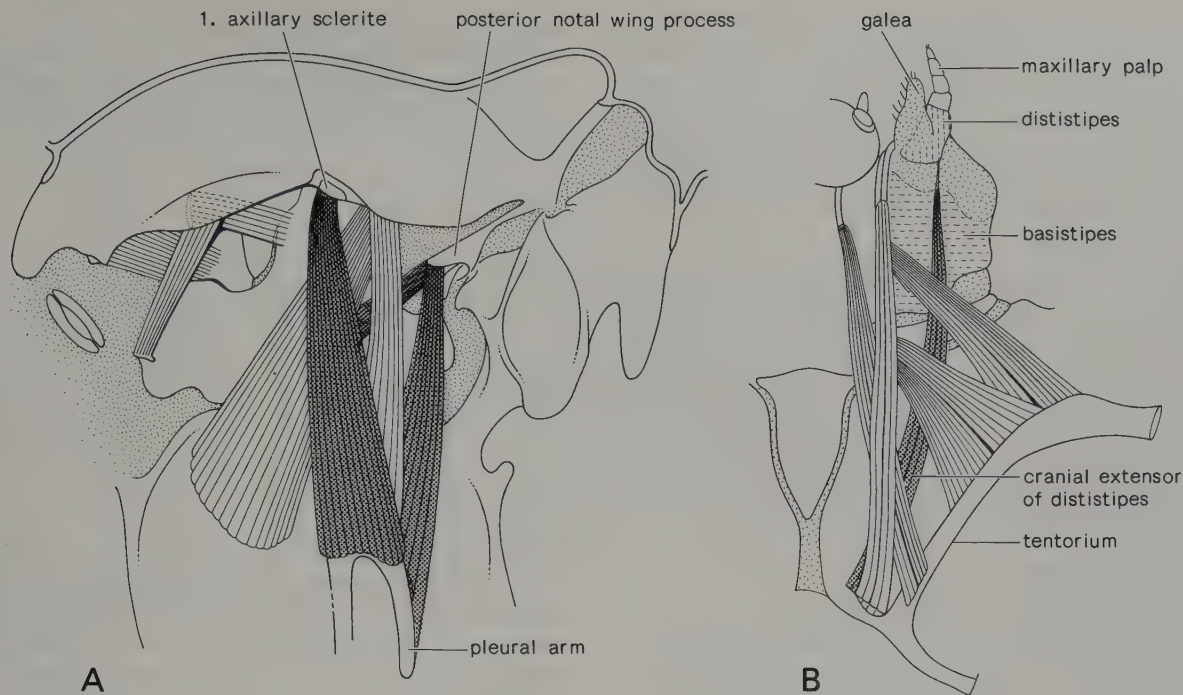


Fig. 5.7 Some structural specialisations (shaded) of the Mecoptera: A, pterothoracic pleurotergal muscles of a panorpid scorpionfly (Mecoptera); B, larval maxillolabium and adjacent cranium of a limnephilid caddisfly (Trichoptera). [A after Mickoleit 1969; B after Das 1937]

Superorder ANTLIOPHORA

Prospina reduced, furca-spinal muscle concomitantly transformed into interfurcal bundle. Larval mouth-parts without lateral labral retractor, hypopharyngeal retractor and ventral salivarium dilator.* Imaginal mandibles (lost in the Siphonaptera) slender, anterior articulations weakly developed or lost. Prelabium without endite lobes/ligula and associated muscles. Winged segments (where present) with posterior notal wing process specialised, bearing insertion of pleural muscle (Fig. 5.7A). More work is needed to elucidate the distribution and structures of sperm pumps within this superorder.

The interrelationships between the antliophoran taxa Mecoptera, Siphonaptera and Diptera remain debated. While a once-suggested position of the Siphonaptera as subordinate within Diptera cannot be upheld (Kristensen 1981), a few traits might support a sister-group relationship between the two, viz. the apodous larvae and the adecticous pupae (the latter are correlated, of course, with the absence of mandibles/mandibular transverse movements in the adults).

It would *a priori* seem very likely that the Mecoptera (*s.lat.*) are paraphyletic in terms of the Siphonaptera, the Diptera or both. The small Southern Hemisphere scorpion fly family Nannochoristidae has recently been shown to stand apart from other mecopterans because of primitive

traits in genital morphology (Mickoleit 1978; Willmann 1981, 1987, 1989) and larval leg structure (Pilgrim 1972; Hinton 1981). Hinton raised this taxon to ordinal rank: Nannomecoptera. Wood and Borkent (1989) have suggested a sister-group relationship between the Nannochoristidae and the Siphonaptera + Diptera; this they supported by the elongately blade-like, primitively toothed lacinia and the absence of a galea in these groups. They further noted the alternative possibility of a sister-group relationship between the Nannochoristidae and the Diptera only, as indicated by the presence in these groups of a conspicuous pit-organ on the 3rd maxillary palp segment. This organ has been lost repeatedly within the Diptera, and thus its absence in the Siphonaptera is easily explained as a loss character. The eversible anal papillae (osmoregulatory) found in the aquatic larvae of nannochoristids and some nematoceran Diptera are similarly easily explained as parallelisms.

On the other hand, there is a suite of derived traits, listed below, that appear to indicate that the Mecoptera *inclusive* of the Nannochoristidae are, after all, a monophyletic taxon (Mickoleit 1981; Willmann 1984, 1987). It remains a very real possibility that the sister-group of the Siphonaptera is the Mecoptera, rather than the Diptera. Putative siphonapteran/mecopteran synapomorphies include the remarkably similar arrangement of close-set, prominently elongate, proventricular acanthae (which Boudreaux 1980 believed to be secondarily lost in the Diptera), sperm axoneme coiling around mitochondrial derivative, absence of extrinsic labral muscles, procoxa with condylus fitting pleural concavity, and 'link plates'

*As noted by Willmann (1989), absence of the tentorial cardo adductor cannot be included among antliophoran autapomorphies (as was stated by Kristensen 1975), since Hinton (1958c) recorded this muscle from the mecopteran family Boreidae.

present adjacent to thoracic spiracles (Schlein 1980; further study of these interesting thoracic features is desirable), and perhaps the sexual dimorphism of the abdominal ganglionic concentration.* The loss of the nine outer singlets in the sperm axoneme may not be a valid synapomorphy of the two groups, since outer singlets have been reported from a bittacid scorpionfly (Gassner *et al.* 1972).

Order MECOPTERA

Clypeolabral articulation obliterated. Tentorio-mandibular muscle reportedly lost (retained in dipteran groundplan). Hypopharyngeal muscles lost (mouth-angle retractor and dorsal salivarium dilator retained in siphonapteran and dipteran groundplans). Gonopod bases fused above and below phallic apparatus. Distal part of gonostylus with membranous organ (Willmann 1981). Larval metathoracic spiracle non-functional (except in last-instar larvae of Siphonaptera and a few Diptera).

Order SIPHONAPTERA

Strongly autapomorphic. Adults apterous, bilaterally flattened, ectoparasitic on homoiothermous vertebrates. Compound eyes small, greatly modified; ocelli absent. Antennae short, in cranial grooves. Sucking mouth-parts with labral and lacinial stylets; mandibles absent. Thorax greatly specialised. Larva apodous.

The long labial palps (with up to five segments) of some adult fleas are intriguing. As noted by Mickoleit (in Hennig 1986), they do create difficulties for the assignment of fleas to the mecoptero-dipteroid complex. The high segment number is aberrant for pterygote insects anyway; possibly this is a case of autapomorphic subsegmentation.

Order DIPTERA

Strongly autapomorphic. Anterior mandibular condyle lost. Labial palps forming labellum. Metathoracic wings transformed into halteres, metathorax much smaller than mesothorax. Metacoxa without discrete meron. Larvae apodous. First larval instars apneustic or metapneustic (see Table 2.2); larval spiracles always devoid of closing apparatus. Several other putative dipteran autapomorphies are discussed by Hennig (1973).

Superorder AMPHIESMENOPTERA

Prelabium fused with hypopharynx, in larva forming projecting lobe with silk gland orifice apically. Secondary furcal arms in pterothorax fused with posterior epimeral margin. One ventral neck muscle originating on fore coxal margin. Wings probably primitively with numerous

hairs; fore wing anal veins primitively looping up into double-Y configuration. Abdominal S5 primitively with openings of prominent glands. Ventral diaphragm muscles inserting on nerve cord. Female heterogametic sex. Altogether close to 20 amphiesmenopteran autapomorphies are now recognised (Kristensen 1984e).

Order TRICHOPTERA

Imaginal prelabio-hypopharyngeal lobe forming large, eversible 'haustellum' with intricate system of canals (formed by modified microtrichia) enabling uptake of fluid nutrients. Clypeolabral articulation and extrinsic labral muscles absent (parallelism with Mecoptera). True mandibular articulation absent. Larvae aquatic, apneustic (see Table 2.2). Larval antennae greatly reduced, without musculature. Larval tentorium exceedingly delicate.

Order LEPIDOPTERA

Adults always without median ocellus. Corporotentorium with posteromedian process. Profurcopleural bridge with prominent free arm. Mesothorax with prominent apodeme issuing from upper part of pleural suture. Protibia primitively with epiphysis for antennal cleaning. Wings covered with broad, coloured scales (modified setae). Phallus protractors primitively originating within gonopods. Cephalic aorta enclosing recurrent nerve; mesothoracic aorta primitively curving towards dorsum. Apyrene sperm generally present. Larval pleurostome elongated, cranio-cardinal articulation far behind mandibular base. Altogether more than 25 possible lepidopteran autapomorphies are now recognised (Kristensen 1984e).

The Amphiesmenoptera seem to provide the best supported instance of a sister-group relationship between two insect orders. It is here suggested that the larval life-style of the lowest Lepidoptera (suborder Zeugloptera) closely resembles that of ancestral Amphiesmenoptera; zeuglopteran larvae are 'soil animals' occurring in very moist situations (bryophyte growths etc.) which would seem to be only a small step away from genuine aquatic habitats.

Section and Order HYMENOPTERA

Imaginal laterocervicale not separate from pro-pre-episternum. Hind wings markedly smaller than fore wings, their costal margin with row of hooks ('hamuli') engaging with bent hind margin of fore wing. Wing venation uniquely modified. Mesothorax with principal flight motor muscles, considerably larger than metathorax. Notocoxal muscles absent and (most probably related to this absence) meron not demarcated on coxae. T1 broadly fused to metanotum; abdominal tergal plates wide, including spiracles and concealing sternal margins. Haplodiploid sex determination. Larval eye (where retained) with single corneal lens overlying several discrete, acone ommatidia.

* Sexual nerve cord dimorphism has also been reported in primitive moths, but it might be restricted to a subgroup within the glossatan family Eriocraniidae (Kristensen and Nielsen 1981a) and hence should not be considered plesiomorphic at the mecopterid level.

Fossil History and the Evolution of Hexapod Structures

J. KUKALOVÁ-PECK

A knowledge of fossil insects can contribute significantly to the reconstruction of ancestral groundplans and to the recognition of primitive and derived character states, especially when combined with detailed analyses of the organs of living forms with respect to their homologues in other arthropods. Both comparative morphology and the fossil record have been used extensively here as bases for phylogenetic inferences. Wing venation is of particular importance in the interpretation of fossils, and in this section the venation of all insect orders has been for the first time fully homologised in a unified veinal system and compared, using a cladistic approach. Throughout the text, reference will be made to the standard geological time scale. The three major geological eras are the Palaeozoic (including the Cambrian, Ordovician, Silurian, Devonian, Carboniferous and Permian periods), Mesozoic (including the Triassic, Jurassic and Cretaceous periods) and Caenozoic (including the Tertiary and Quaternary periods). The Tertiary period is further subdivided into five epochs (Palaeocene, Eocene, Oligocene, Miocene and Pliocene) and the Quaternary into two (Pleistocene and Holocene or Recent). Strata that are older than the beginning of the Palaeozoic (Cambrian) are usually called Precambrian. Those periods most relevant to hexapod evolution (Carboniferous to Cretaceous) are often subdivided, but the names of these stages differ among American and European geologists. In America, the Carboniferous is usually divided into an earlier Mississippian and later Pennsylvanian. The only subdivisions used here are Lower (early), Middle and Upper (late), abbreviated L., M. and U., respectively. Table 6.1 summarises the occurrences of the hexapod orders in the fossil record and gives estimates in millions of years of

the time elapsed since the beginning of each era, period and epoch. Throughout the discussions mention will be made of important fossil insect localities, especially in the Northern Hemisphere (Australian sites are discussed below). Major Palaeozoic localities in the U.S.A. are in Illinois (Mazon Creek; U. Carboniferous, Westphalian D) and New Mexico (U. Carboniferous-Permian boundary) and in Kansas (Elmo) and Oklahoma (L. Permian). In Eurasia, significant Palaeozoic sites are in France (Commentry and Montceau-les-Mines; U. Carboniferous, Stephanian), West Germany (Hagen-Vorhalle; U. Carboniferous, Namurian B), Czechoslovakia (Obora, Moravia; L. Permian) and the U.S.S.R. Russian Palaeozoic sites include: the Kuznetsk Basin, east of Novosibirsk in Siberia (Carboniferous and Permian); the Soyana River, near Arkhangelsk (U. Permian); and the Ural Mountains region (Tshekarda on the Sylva and Tshekarda Rivers, L. Permian; Kargala near Orenburg and Tikhie Gory on the Kama River, U. Permian). Mesozoic localities are mainly in the U.S.S.R., but some are located in Mongolia and China. The Soviet localities include: Issyk-Kul, a lake in the Tien Shan Mts of Kirgizia (Triassic and Jurassic); Fergana, Tadzhikistan, Central Asia (M. Triassic); the Kuznetsk and Irkutsk basins in Siberia (Jurassic); Karatau, between the Aral Sea and Lake Baikal in Kazakhstan (U. Jurassic to Cretaceous); Transbaikalia near the Mongolian border (U. Jurassic to Cretaceous); and the Taimyr Peninsula in northern Siberia (Cretaceous amber). Several rich Jurassic and Cretaceous localities occur in Mongolia and China. The area extending from the Ural Mts to China is usually referred to as Angara, and the Permian and Mesozoic fauna and flora are considered to have been distinct from those of western Europe

and North America. The Southern Hemisphere land mass existing during the same time period is referred to as Gondwana. Modern summaries of palaeontological data with full references, have been given by Carpenter (in press), Crowson *et al.* (1967), Hennig (1981), Kukalová-Peck (1978, 1983, 1985, 1987), Ponomarenko (1988), Rasnitsyn *et al.* (1985), Riek and Kukalová-Peck (1984), Rohdendorf (1962), Rohdendorf and Rasnitsyn (1980) and Wootton (1981b).

GENERAL FOSSIL RECORD

Cambrian – Devonian. It is thought that the Crustacea are the sister group of the Tracheata (Myriapoda plus Hexapoda), and since relatively advanced Crustacea occurred in the Cambrian, ancestral tracheates presumably were also present by this time. The generalised, common ancestors of myriapods and hexapods are not yet known. Since terrestrial life was not possible before the Ordovician, it is presumed that the ancestral Precambrian and Cambrian tracheates were, like the Crustacea, aquatic. Marine myriapod-like animals are known from the L. Silurian of Wisconsin, U.S.A. (Mikulic *et al.* 1985 and unpubl.) and terrestrial ones occur in the U. Silurian of England and Scotland (Rolfe 1980). The first known hexapods are collembolans; *Rhyniella praecursor* and other species found at the base of L. Devonian in Scotland, were well advanced and some resemble Recent Isotomidae and Neanuridae (Greenslade 1988). The same strata also produced *Rhyniognatha hirsti* (Tillyard 1928b), known only from dicondylous mandibles of the type found in Monura, Thysanura and Pterygota, and an undescribed pterygote nymph (Kühne and Schlüter 1985). Fragments of Archaeognatha occur in the L. Devonian of Quebec (Labandeira *et al.* 1988) and in the M. Devonian of Gilboa, New York (U.S.A.) (Shear *et al.* 1984), together with mites, amblypygids, opilionids, scorpions, pseudoscorpions, centipedes, arthropleurids, trigonotarbid and spiders. Obviously, the terrestrial arthropods must have radiated very early, probably in the Ordovician (Kukalová-Peck 1987). Unfortunately, Ordovician and Silurian freshwater deposits are extremely scarce.

Land plants, including vascular types, probably occur at least in the U. Ordovician (Gray *et al.* 1982). Before that, floating mats of bacteria, blue-green algae and true algae protruding from water and decaying on shores, and fungi, offered the only semiaquatic or terrestrial habitats and food. Ordovician and Silurian plants were of low stature, and offered interstitial spaces but provided almost no litter. Probably the vegetation was very patchy and early hexapods dispersed on foot, or by means of strong winds or rafting. Predator pressure must have been enormous and was almost exclusively from other arthropods, such as arachnids and myriapods. The oldest Ectognatha, Archaeognatha, Monura, Thysanura (*Zygentoma*) and ancestral Pterygota were free living. Therefore, selection favoured the preservation of the original arthropod, leg-derived appendages serving escape rather than hiding strategies. Adaptation for cryptic life, hiding and feeding in confined spaces, occurred twice in early hexapods: in

the early branch Parainsecta (Collembola-Protura) and later in the Insecta: Entognatha (Diplura). This resulted independently in the progressive reduction of eyes and leg-derived appendages, and the enclosure of the mouth-parts (Kukalová-Peck 1987). Trees first occurred in the U. Devonian, long after the insects must have radiated into all major groups and long after the appearance of the pterygotes.

Carboniferous. In the L. Carboniferous, or probably even earlier, pterygotes radiated into the stem groups (see p. 153) of all major lineages, one extinct (haustellate Palaeoptera) and seven surviving (ephemeroids, odonotoids, plecopteroids, orthopteroids, blattoids, hemipteroids and endopterygotes). Unfortunately, L. Carboniferous freshwater deposits are very rare and no published insect record is available until the U. Carboniferous. In sediments deposited at this time, fossils (especially isolated wings) of tropical lowland insects are fairly common and varied, but mountain faunas are not known. Carboniferous insects are unfamiliar looking to entomologists and difficult to classify in a comprehensive system (Carpenter 1971). Most fossils come from a broad, warm and humid tropical belt of the then equatorial regions of Europe, North America and eastern Asia, but there is a lesser record from the temperate zone of Angara (Kuznetsk Basin), Argentina, Zimbabwe and Tasmania, and several cockroaches have been recorded from India. Carboniferous Palaeoptera were about as common as Neoptera, and included Protodonata, Ephemeroptera and palaeodictyopteroid orders. The Protodonata were diverse, abundant and adapted for catching large prey. Protodonata and Ephemeroptera had primitive aquatic nymphs with gills, and adults of some were gigantic with wingspans of 71 cm and 45 cm, respectively. Haustellate palaeodictyopteroids (Diaphanopteroidea, Palaeodictyoptera, Megasecoptera and Permothemistida) were dominant; they had powerful, sucking beaks up to 30 mm in length and wingspans up to about 56 cm. Palaeodictyopteroid nymphs were terrestrial with sucking mouth-parts and were often flattened and highly sclerotised, or shrouded in peculiar, long outgrowths (Kukalová-Peck 1971, 1972, 1973, 1985). Carboniferous Neoptera are preserved mostly as isolated wings, but the plecopteroids, orthopteroids, blattoids, hemipteroids and endopterygotes are all definitely represented. Many plecopteroids had aquatic young nymphs, but some older nymphs were terrestrial. The orthopteroids had already acquired jumping hind legs. Parts of blattoids, especially cockroach-like tegmina, are the most frequently found insect fragments. The composition of the Carboniferous entomofauna and its interactions with plants were very different from today, because more than 50% of the species had sucking or semi-sucking mouth-parts compared to less than 10% in the Recent fauna. Haustellate palaeodictyopteroids imbibed mostly spores from loose cones (probably mainly of lycopods) or juices (probably from large ovules of Cordaitales and pteridosperms). Ancestral hemipteroids with a highly domed postclypeus displayed an astonishing variety of chewing-sucking and stylet-bearing mouth-parts. The oldest Carboniferous

holometabolous insects lived in the tropics, but they are represented largely by isolated wings, which are difficult to identify. An eruciform-like, polypodous larva of the mecopterid-hymenopterid type, which would have required a pupa to turn into adult, was recently found in the U. Carboniferous of Illinois (Fig. 6.26A). Most Palaeozoic nymphs had articulated wings, as shown by winglets preserved at various angles, and some were very probably capable of active flight (Kukalová-Peck 1983, 1987). Biomechanical calculations confirm that even small wings, *if articulated*, may have been useful for flying and functionally intermediate between a proto-wing and an accomplished wing blade (Wootton and Ellington in press). Proto-wings probably functioned initially as respiratory organs in amphibious or aquatic conditions (as do the flattened exites of other arthropods), and subsequently became used to escape predators (Kukalová-Peck 1983, 1985, 1987).

Wingless, extinct *Monura* were very abundant in some deltaic habitats. Like *Archaeognatha*, they probably jumped away from predators by contracting abdominal musculature. Silverfish (*Thysanura*) reached a gigantic size (6 cm in body length) and used long bristles on abdominal leglets, cerci and the cercal filament as an alarm device sensitive to air movements.

Permian. During this period, progressive aridity in the Northern Hemisphere and glaciation in the Southern Hemisphere induced well defined climatic zones and dramatic changes in flora and entomofauna. Large lycopods became extinct, and ferns, pteridosperms and Cordaitales in drier regions were gradually replaced by gymnosperms. Insects experienced rapid evolution and probably reached their richest diversity then. Large, sucking palaeodictyopteroids survived in lowland forests well into the Permian, but mostly decreased in size. Predacious Protodonata were extremely varied and even increased in size. Large, primitive Neoptera mostly became extinct. Many small 'Permian' insects very probably had evolved in association with xerophilous plants on mountain ridges during the Carboniferous, but are not represented among Carboniferous fossils. In the L. Permian, explosive radiation of holometabolous insects occurred world-wide. Near the equator, located in what is now the Northern Hemisphere, extreme variations in local climate promoted diversity. The cool-temperate zones of Gondwana and Angara had impoverished entomofaunas restricted mainly to Auchenorrhyncha and Coleoptera, but with some neuropterids and mecopterids and many Protelytroptera (ancestral earwigs). In the Southern Hemisphere, sporadic L. Permian insects are known from South America, Zimbabwe and Zaire, and U. Permian ones from Australia, Antarctica, Brazil, the Falkland Is and Madagascar (Tillyard 1928a; Riek 1973c, 1974c; Tasch and Riek 1969). Australian Auchenorrhyncha were smaller and more diverse than those of Angara, but South Africa was warmer than Australia and had the richest Permian homopterous fauna. Permian insects look familiar today and mostly can be assigned readily to the ancestral groups of Recent orders. However, they represent a maze of side branches. Occurrences of Recent families in

the Permian are controversial. Triassic insects were to emerge as a small, seemingly random sample from an extremely rich late Palaeozoic entomofauna, which was abruptly cut down by the Great Permian Extinction.

Mesozoic. The Triassic was generally arid and warm in the Northern Hemisphere. In the Jurassic and Cretaceous, a warm climate prevailed and advancing marine transgression covered continents. After various extinctions, the remaining Mesozoic plants and insects became relatively modern in appearance. Forests contained mainly cycads and conifers, with multiple protective devices against insects and a ground cover of ferns. Only a few Palaeozoic insect orders survived: the Protodonata became extinct in the Triassic, Paraplecoptera, Glosselytrodea and Miomoptera in the Jurassic, and Protelytroptera in the Cretaceous. Triassic higher taxa are mostly groups at the bases of Recent lineages, but some taxa are placed in extant families. Many Recent families started in the Jurassic. In the Cretaceous, angiosperms and deciduous trees became increasingly dominant. M. Cretaceous forests were fundamentally modern. Angiosperm-associated Cretaceous insect families probably originated (unrecorded) in the Jurassic. By the Cretaceous most modern families were already extant and insect sociality had evolved (Burnham 1978). The effects of the global biocoenotic crisis of the M. Cretaceous on insect evolution have been discussed by Rasnitsyn (in Ponomarenko 1988) and Whalley (1988a). The Triassic record of Europe and America is poor or unworked, but that of the U.S.S.R. (Tien Shan, Central Asia), Australia and South Africa is extensive and well documented. A rich Jurassic record is available, especially from England, West Germany, U.S.S.R. (Kazakhstan and Siberia), China and Mongolia. Cretaceous insects are numerous and are found especially in Australia, Lebanon, Mongolia, Siberia, China, England and Brazil. U. Cretaceous amber fossils are plentiful in Canada.

Tertiary. Tertiary insects are essentially modern and include mostly genera indistinguishable from those of the Recent fauna. Insects occur frequently in freshwater deposits, such as the Oligocene shales from Florissant, Colorado (U.S.A.), and also in Eocene-early Oligocene Baltic amber (Kellner-Pillaut 1970), Oligocene amber from the Dominican Republic, and Miocene amber from Chiapas, Mexico. Tertiary first occurrences in the fossil record are often a result of sampling bias, and it is likely that orders such as Phthiraptera and Strepsiptera originated long before the beginning of the Caenozoic. Modern Lepidoptera are dependent on angiosperms, but most primitive forms had chewing mouth-parts and ate pollen which existed already in the Palaeozoic. Mesozoic and Tertiary faunistic complexes were studied by Zherikhin (1978).

EVOLUTION OF HEXAPOD STRUCTURES

Groundplan of Hexapod Leg

There is now evidence that the hexapod leg evolved from an ancestral arthropodan leg which contained in its groundplan no fewer than 11 segments and an unknown

number of outer and inner rami or annulated lobes (Kukalová-Peck 1987). The outer rami or *exites* are evaginations of the intersegmental membrane; they are articulated and moved by muscles from the preceding and following leg segments, and they often function in respiration (as gills), movement (as swimming paddles) or sensory perception. The inner rami or *endites* are segmental outgrowths, detached and hinged, and muscled primitively only from the parental segment. They provide the working parts for the mouth and genitalia, and serve as abdominal vesicles (E. L. Smith in Kukalová-Peck 1983, 1987) (Figs 6.1–3, A, B, 9B, 10, 21A, B).

Thoracic legs (Fig. 6.2A, left) were long believed to consist only of 6 segments: coxa (CX), trochanter (TR), femur (FE), tibia (TI), tarsus (TA) with 5 subsegments, and pretarsus (PT). This scheme is incomplete and does not allow leg-derived structures to be homologised among the hexapods, myriapods, and other arthropod groups. A more useful scheme (Figs 6.1, 2A, right, 3A, B) recognises additionally: prefemur (PFE), patella (PAT), subcoxa (SCX, forming the thoracic pleuron and participating in the abdominal pleuron), basitarsus (BT), epicoxa (ECX, forming the wing articulation in the thorax but fused to the tergum in the head capsule and abdomen), up to five thoracic and one abdominal epicoxal exite (ex), and two pairs of endites (end, on CX and TR) (Kukalová 1969b–70b; Kukalová-Peck 1983, 1985, 1987; E. L. Smith 1988c and Kukalová-Peck 1983). This new reconstruction of the leg groundplan with 11 segments, at least 5 exites and 2 or more endites, allows homologies to be recognised relatively easily among the terrestrial and

other arthropods (Figs 6.1, 2A, 3A, B). This groundplan leg and all other arthropod appendages can be derived from the segmented, polyramous limb of the Precambrian, aquatic, common ancestor of all arthropods.

Manton (1977 and ref.) argued that arthropods are polyphyletic, with the Tracheata and Onychophora being closely related and forming the 'Uniramia'. Manton was misled by the legs of Recent arthropods, which have such reduced segmentation that they cannot be compared directly with one another. Manton did not examine whether or not they could be derived from a single ancestral groundplan with many segments, which would show the legs to be homologous and thus allow monophyly for the Arthropoda. Instead, she stressed their differences. The legs of Crustacea are polyramous (with several serial exites), as are the legs of all other arthropod groups, but Manton emphasised only one conspicuous coxal exite adapted for swimming and considered the crustacean to be 'unique' and 'biramous' (nevertheless a coxal exite also occurred in most early chelicerates and trilobitiforms, Fig. 6.1A). Manton insisted that insect legs were uniramous (i.e. lacking exites), even though modern bristletails have coxal exites (rami), and explained insect palps and the various exites and endites as 'neoformations', even though the palps of some living and many fossil insects are demonstrably leg-like and even end in double claws (Kukalová-Peck 1983, 1985, 1987; E. L. Smith 1988c).

Onychophora eat with mandibles formed from the tips (claws) of their lobopodial legs, while Arthropoda eat with the upper part (gnathobase) of the leg (Fig. 6.1A).

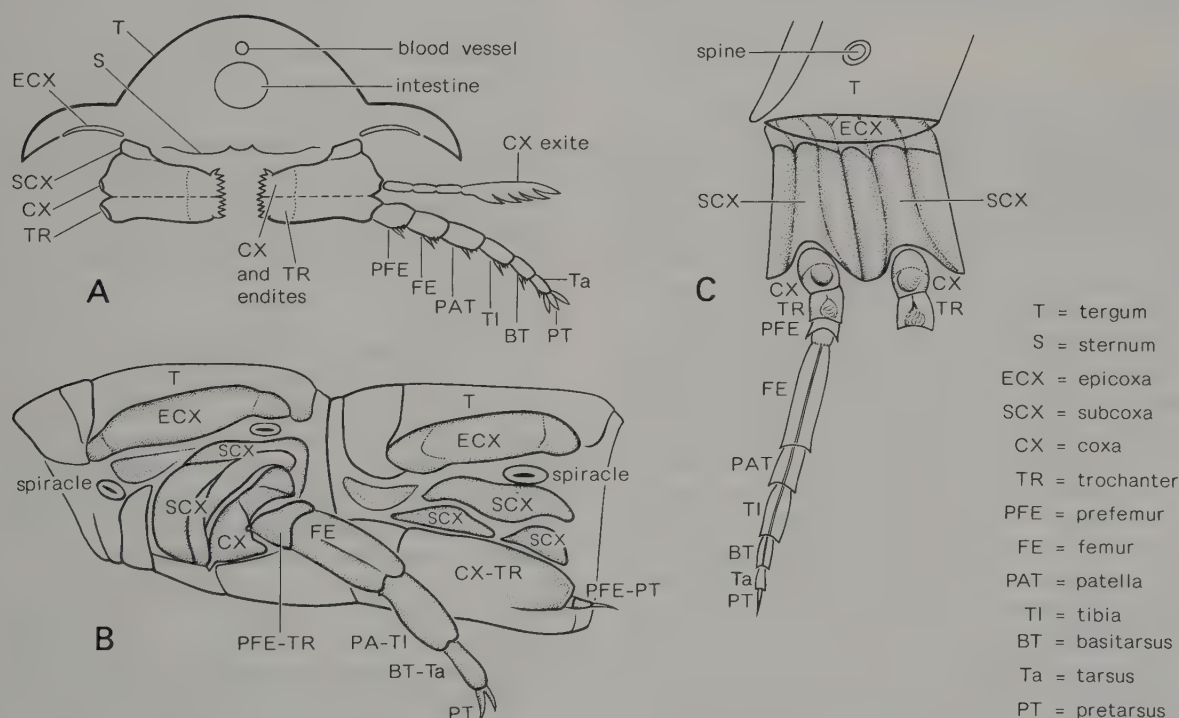


Fig. 6.1 Homologous leg segments in trilobites, insects and myriapods. A, transverse section (diagrammatic) of trilobite body segment illustrating gnathobase (homologous to insect mandible), free leg (homologous to insect palp) and respiratory exite on coxa. B, *Heterojapyx* sp., Insecta-Diplura, mesothorax and abdominal segment 1. C, composite diplosomite based on *Acantherpestes* sp. and *A. vicinus*, Diplopoda, U. Carboniferous of Illinois and Czechoslovakia, respectively. [A by J. Kukalová-Peck; B, C, after Kukalová-Peck 1983]

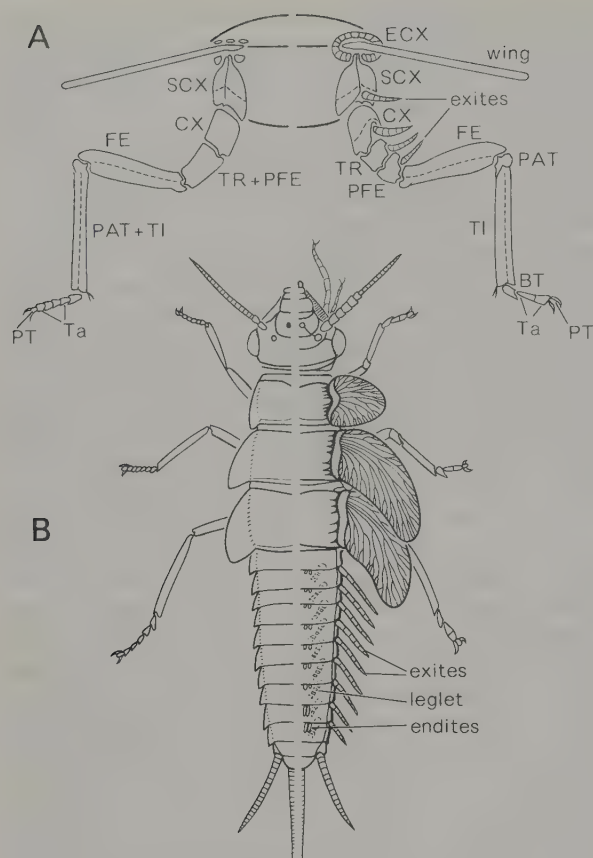


Fig. 6.2 A. Thoracic leg segment and leg-derived appendages, and B, nymphal morphology, as they occur in most Recent winged insects (left) and in the most primitive Palaeozoic pterygotes (right). Lettering as in Fig. 6.1 [J. Kukalová-Peck]

Manton observed that in some myriapods (Diplopoda and Chilopoda) the mandible is segmented and concluded erroneously that it represents a complete leg with claws, as in the Onychophora. In fact, the gnathobase of Trilobita, Chelicerata and Crustacea, the myriapod mandible and the hexapod mandible are *all* composed of several, identical leg segments, namely SCX, CX and TR, and of two endites (CX and TR) serving as teeth (in insects, molar and incisor). In the gnathobase and the hexapod mandible, all these segments are fused, but in Diplopoda and Chilopoda, they remain largely unfused (E. L. Smith, in Kukalová-Peck 1983). The free part of the mandibular leg or *telopodite* was retained in Crustacea and Trilobita (Fig. 6.1A) but lost in Tracheata, where it is retained as a palp only in the maxilla and labium. In contrast, the leg of Onychophora is a primitive, regularly constricted (annulated) lobopod which lacks definitive segmentation. Probably the Onychophora are related to Tardigrada, and the common ancestors of both emerged from an assemblage which also gave rise to the Arthropoda.

Significant transformations of the leg segments seen in the hexapod groundplan are as follows (Figs 6.1B, 2, 3) (Kukalová-Peck 1983, 1987; E. L. Smith 1988c). The epicoxa (ECX) is fused with its corresponding tergum in the

head and abdomen, and sometimes in the thorax; primitively, the epicoxa is still separated from the tergum by a suture (Figs 6.9, 10, 19E, F). In the pterygote thorax, the epicoxa surrounding its flattened exite (proto-wing) became subdivided into closely packed sclerites attached to numerous leg muscles, and became the wing articulation (Fig. 6.3A, C, 10F, 12A, B, 13D, 15D). The subcoxa (SCX) of each thoracic segment spread flat into the membranous lateral wall of the segment, forming a sclerotised reinforcement (pleuron). In Archaeognatha, the primitive SCX on the mesothorax and metathorax is still an independent leg segment and does not support the membranous wall (the so-called 'pleuron' of bristletails belongs to the epicoxa). Thysanura have their pleuron (SCX) secondarily desclerotised and fragmented (as in many other tracheates) into crescents along musculature boundaries, to accommodate their peculiar leg movement. The abdominal pleuron of Insecta (including Diplura) is composed of the fused and flattened SCX and CX and TR, while abdominal leglets and gonostyli (as well as palps) consist of PFE, FE, PAT, TI, BT, subsegmented T, and PT with double claws (Figs 6.1B, 3A, 9A). All these segments are articulated. Parainsecta have only SCX incorporated into the abdominal pleuron, while CX and TR mostly remain in the form of articulated segments. Thoracic free legs articulate by means of CX; TR and PFE are separate in many fossils but otherwise fused. In all hexapods, the thoracic patella is fused to the tibia and the tarsus is primitively subdivided into 2 subsegments. A tarsus with 2 subsegments occurs also in all palps, abdominal leglets and cercal leglets of primitive groups; thus a thoracic tarsus (TA) with 4 subsegments is generally a derived condition. Double claws on PT are primitively present in all palps, legs, leglets, gonostyli and in cercal leglets (Fig. 6.3A, 9); therefore one claw represents a derived condition in Hexapoda. Several leg segments may be secondarily subdivided (e.g. CX of the labrum and labium, SCX of the thoracic pleuron, and many thoracic tarsi with up to 4 subsegments).

Groundplan of Hexapod Head

The hexapod head and its leg-derived appendages were compared with those of all other arthropods by E. L. Smith (1988b), and a reconstruction of its groundplan integrating evidence from extant and fossil species was proposed by Kukalová-Peck (1983, 1985, 1987) (Figs 6.9C, D, 10A, 14C, 15E, F). According to this reconstruction, the head is composed of 6 segments separated by sutures and bearing 6 pairs of leg-derived appendages. An acron is absent in all Arthropoda. Six terga have fused with 6 pairs of epicoxae to form the head capsule. Ocelli and eyes occur at the edges of the terga, on a suture between the tergum and epicoxa (as in trilobites). Segment 1, the labral segment, has an almost triangular tergum and 2 triangular epicoxae; a clypeolabrum is formed by a fused first pair of coxopodites (SCX, CX and TR), which have partially receded into the head capsule; CX endites became epipharyngeal lobes, and TR endites form the tip of the labrum (e.g. triangular archilabrum in palaeodictyopteroids, Figs 6.10A, 14C, and in Hemiptera,

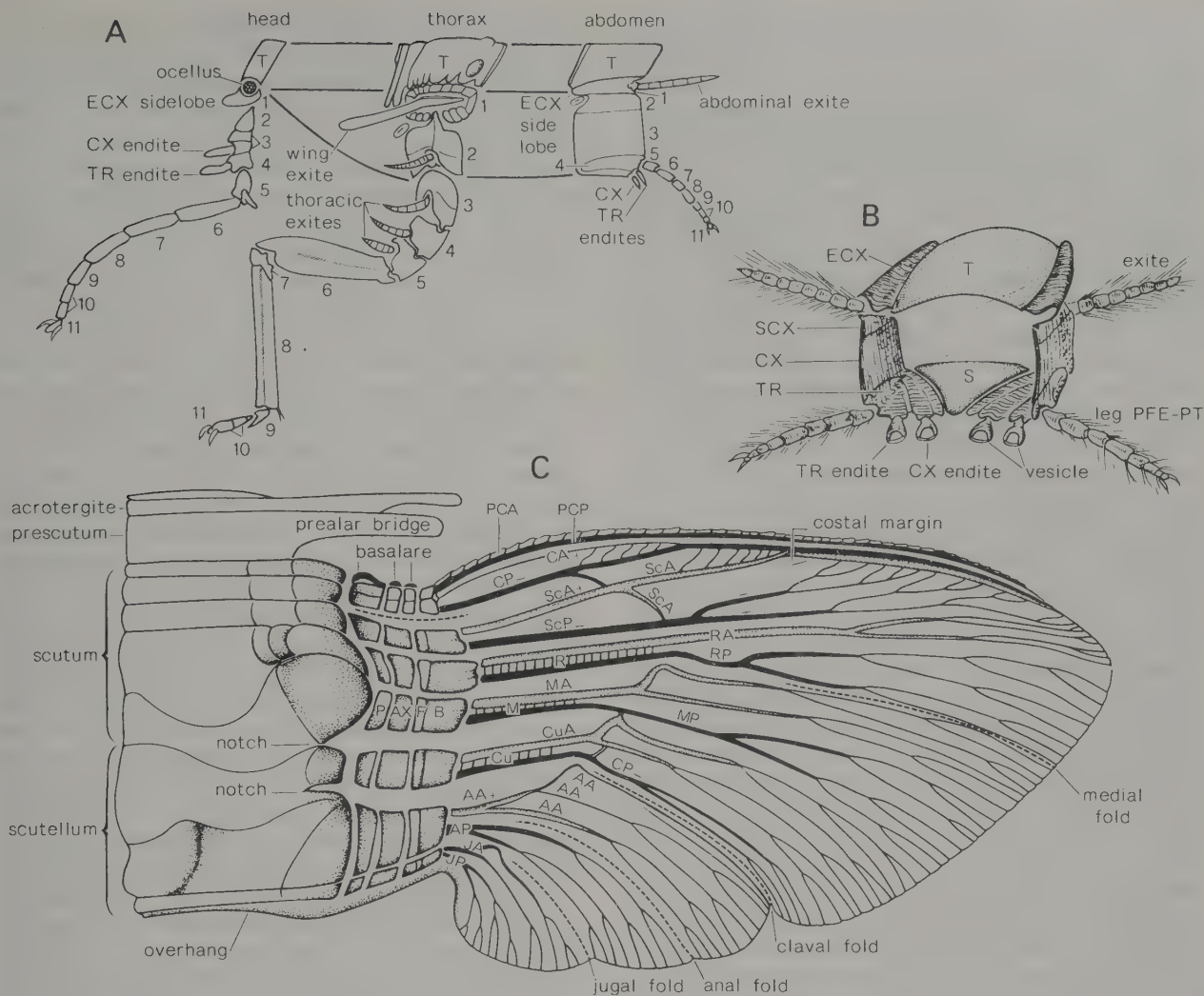


Fig. 6.3 Groundplans of the insect head, thorax and abdomen, as documented by the Palaeozoic fossil record: A, leg involvement in the head, thorax and abdomen. Lettering as in Fig. 6.1. Free or mobile leg articulated in head by SCX (2), in thorax by CX (3) and in abdomen by PFE (5); thoracic pleuron (wall reinforcement) formed by SCX (2), abdominal pleuron by SCX, CX and TR (2–4); exites tactile, locomotory (wings) or respiratory (gills); endites (CX and TR) form working parts of head and genitalia. B, pre-genital abdominal segment with triangular sternum and 4 pairs of leg-derived appendages. C, scheme of pterygote wing venation, with articulation, complete venal system, folds, venational braces and venal fusions; the ancestral articular band of unfused sclerites (P = proxalare, AX = axalare, F = fulcalare, B = basivenale) gave rise to all Recent types of wing articulation.

[A, B after Kukalová-Peck 1987; C after Kukalová-Peck 1983]

Fig. 6.22B). All sulci crossing the clypeolabrum are secondary, serving as reinforcements and flexion lines. Segment 2, the antennal segment, bears a pair of antennae, each of which represents an entire leg beginning with SCX and primitively 8-segmented (as they are in Diplopoda); 6 antennal segments (with extrinsic leg musculature) are retained in Parainsecta (some Collembola), but in Insecta (including Diplura) all except the basal 2 segments (SCX, CX) have become flagellar and annulated and all have lost their extrinsic musculature. Segment 3, the postantennal or cheliceral segment, is fused with segment 2, and its leg-derived appendages, the superlinguae (homologous to the second antennae in postlarval Crustacea) are internal, have intrinsic endite muscles and may combine with adjacent sternum 4 to form a hypopharynx. Segment 4, the mandibular segment, of Pterygota may have a subdivided tergum (pericranial cari-

na); the mandible is a coxopodite (SCX, CX and TR fused) articulated by the subcoxa, and the endites of CX and TR serve, respectively, as molar and incisor lobes (the palp is lost in Tracheata). Segment 5, the maxillary segment, bears a maxilla consisting of a cardo (SCX), by which it is articulated, a stipes (CX fused with TR in Pterygota and Archaeognatha but unfused in Thysanura), a lacinia and galea (CX and TR endites), and a palp composed of PFE, FE, PAT, TI, BT, subsegmented TA, and PT with 2 claws. Segment 6, the labial segment, has two coxopodites (SCX + CX + TR) basally fused with each other and S6, with one (or more) secondary transverse hinges; the paraglossae and glossae are CX and TR endites; the palps are formed in the same way as those on the maxilla. Two ocelli occur on segment 1 (where they are fused to form a single median ocellus) and on segment 2. Eyes are present primitively on segment 2+3 in

Parainsecta (Collembola) but have shifted to segment 4 in Insecta.

Mandible. The most primitive insect mandible is seen in Archaeognatha (Monocondylia). In these the narrow mandible has only one (posterior) articulation, a condyle on SCX, and is therefore capable only of milling action. Faint limits of the original leg segments (SCX, subdivided CX, TR and 2 endites) still persist in the mandibles of Recent Archaeognatha and some Collembola. The derived mandible of Dicondylia (Monura, Thysanura, Pterygota) extends forward to articulate also anteriorly with the labral segment (clypeo-tentorium) and is much broader. This double articulation allows transverse movement (shearing) necessary for predation and crushing hard food. The anterior articulation consists of a loose, non-permanent pivot, a depression or tongue-and-groove sliding articulation, or a permanent pivot.

In the non-permanent mandibular anterior articulation of Monura, Thysanura, Ephemeroptera and palaeodictyopteroids, the mandible sometimes can be disconnected at will and can revert to milling (as in Myriapoda). Thysanura (Fig. 6.9D) had a clypeo-tentorial 'yoke' formed by two knobs which fitted into paired sockets on the mandible, a condition which was probably close to the groundplan of Dicondylia; only the outer socket remained in other insects. Monura (Fig. 6.9C) had a tear-shaped depression on the mandible and a tubercle on the clypeo-tentorium. Ephemeroptera (all nymphs and Palaeozoic adults) (Fig. 6.14C) had the socket expanded into a groove and had a track on the back of the clypeus forming a sliding articulation. Palaeodictyopteroids (Fig. 6.10A) had a conspicuous, long sliding articulation and a groove between the molar and the mandibular blade. Development of a non-permanent articulation instigated very diverse, often autapomorphic, adaptations of the pivot and mandible.

A permanent articulation of the mandible was achieved by developing a tighter fit (ball and socket) of the single, non-permanent pivot such as that seen in Monura. It originated first as an apomorphic character of Neoptera, and secondly in the odonatoids (Odonata and Protodonata), undoubtedly in connection with predation. The permanent condyle allowed powerful mastication and the exploitation of new food sources. Although the change to a permanent pivot was relatively simple, it was apparently irreversible. All further mandibular adaptations in Neoptera follow a totally different path to those in mandibles with non-permanent pivots.

Groundplan of Wing Articulation

The wing articulations throughout the Pterygota were homologised by Kukalová-Peck (1983). The most primitive pterygote wing articulation is here believed to be a densely crowded band of articulated sclerites surrounding the wing like a horseshoe (Figs 6.2A, 3A). The individual dorsal sclerites are similar in size and form 8 rows each of 4 sclerites: *proxalaria*, *axalaria*, *fulcalaria* and *basivenalia*. These rows cover blood channels and the distal sclerite of each row (*basivenale*) is also a blood sinus for one of the 8 veinal pairs (Figs 6.3C, 10F, 12A, B, 15D, 16).

Basivenalia were originally subdivided to accommodate the anterior and posterior veinal sectors. This band of articulated sclerites, exhibiting numerous muscle attachment sites, occurs in all Palaeoptera, but only in the extinct Diaphanopteroidea are the sclerites completely unfused (Fig. 6.10F). By contraction of leg muscles and crowding and slanting the sclerites in the anal and cubital rows the wings could be flexed backwards. The diaphanopterid articulation is very probably close to the groundplan of both Palaeoptera and Neoptera, in which proto-wings were still highly and simply mobile. In all remaining Palaeoptera, several sclerites fused into an articular plate, which in turn fused rigidly with the radial and other veins of the wing. This created a lever pivoting on the pleuron and preventing the wings from flexing backwards, thus allowing them to maintain effortlessly a permanent gliding position. The number of sclerites involved in the articular plates of Palaeoptera varies considerably and has been subjected to autapomorphic changes. The articular plate of early Palaeodictyoptera contains the basivenalia and fulcalaria of Sc and R, while that of later forms (Fig. 6.12A) includes those of M, Cu, A and J as well. The articular plate of Ephemeroptera (Figs 6.14E, F) consists of the basivenalia and fulcalaria of Sc, R and M, with those of Cu, A and J stiffly hinged posteriorly; two columns of free sclerites (proxalaria and axalaria) are articulated mainly in rows aligned with veins in Palaeozoic mayflies, but this pattern is disrupted by desclerotisation in Recent forms (Fig. 1.17B), which may still retain fulcral musculature. Odonatoids have two articular plates: the anterior articular plate of Protodonata (Fig. 6.15D) is composed of the fulcalaria and axalaria of PC and C, fused ventrally and anteriorly with basalaria. This plate still has the original sclerites delimited and partially movable. In Odonata (Fig. 1.17A) these sclerites are completely fused. The posterior articular plate in Odonata is the broadest among Palaeoptera and consists of the basivenalia, fulcalaria and axalaria of Sc, R, M, Cu, A and J. The axalaria are sharply separated by sutures in Protodonata and in some Odonata. The fulcalaria are marked off by a series of muscle attachments in Protodonata and Odonata. One column of free proxalaria lies in between the articular plates and the notum. The costal proxalare is very differently shaped in Protodonata (6.15D) and Odonata (1.17A).

The neopterous wing articulation can be derived only from a completely primitive, unfused band of articular sclerites such as presumed in ancestral Pterygota, before the split into Palaeoptera and Neoptera. The axillary sclerites (1Ax, 2Ax, 3Ax, 4Ax), and the median and humeral plates, have completely different compositions than any of the 'humeral' and articular plates of Palaeoptera. Most neopterous sclerites are formed by specific clusters (Fig. 6.16) with a fixed number of original ancestral sclerites, with the following composition: humeral plate (basivenale and fulcalare of PC + C); 1Ax (proxalare of M, axalare of R, axalare and fulcalare of Sc); 2Ax (axalare of M and fulcalare of R); 3Ax (axalaria and fulcalaria of Cu, A and J). The proxalaria of A and J may form a fourth axillary (4Ax), but more often they are rigidly hinged or

fused to the notum to form a posterior wing process. An additional sclerite, the median plate (fulcrum of M) is articulated with 2Ax and the medial basivenale; a second median plate (composed of the basivenalia of R, M and Cu) may also be present. The 3rd axillary (3Ax), which pivots, rotates and folds upon itself while the wing is flexed backwards, is a unique, sophisticated adaptation. Gliding became possible in Neoptera only after the development of special wing-locking devices, which evolved many times.

Groundplan of Wing Venation

Wing veins probably evolved from densely, dichotomously branched, cuticular ridges that serve to strengthen and distribute blood in flat, movable, leg-derived arthropodan appendages, such as the telson plates in Crustacea (Kukalová-Peck 1983). Clues from comparative studies involving all fossil and living orders indicate that the groundplan of wing venation (Fig. 6.3c) consists of not less than 8 veins, each arising from a particular, subdivided *basivenale* (pl., *basivenalia*) or sclerotised blood sinus: precosta (PC), costa (C), subcosta (Sc), radius (R), media (M), cubitus (Cu), anal (A) and jugal (J). In the proto-wing or groundplan wing, each vein was composed of two sectors, a convex anterior sector (A+), and a concave posterior one (P-), which diverged at the very base, and then branched dichotomously, about 3 times. In later wing blades, sectors A and P often became basally adjacent or superimposed and then fused into a common stem ('stemmed') (e.g. RA + RP formed R). Primitive wings were richly, dichotomously branched and both the sectors and the cuticle between their branches were weakly fluted. In derived wings the pattern of primary branching may be either enriched or impoverished and the fluting more or less pronounced or lost (levelled or flattened). Each sector in the proto-wing divided dichotomously, first into branches 1 + 2 and 3 + 4 (e.g. CuA₁₊₂, and CuA₃₊₄), then into sub-branches (e.g. CuA₁, CuA₂, CuA₃, and CuA₄). There are no odd numbers of branches in a dichotomous system. Where odd numbers seem to occur, they represent always secondary patterns. Pectinate branching is derived. Homologisation of the entire veinal system for all orders requires the use of consistent symbols for all veins, including those which are weak and suppressed in most living orders (e.g. costa posterior, CP-; and subcosta anterior, ScA+). The customary successive numbering of anal veins impedes homologisation; thus anal anterior (AA+) and anal posterior (AP-) are used here. The term radial sector or 'Rs', often used for the radius posterior, has been changed to RP. The term 'postcubitus' ('PCu') (Snodgrass 1935) is a misinterpreted AA, or sometimes AA₁₊₂, which has been cut off from the anal basivenale by a fold and thus appears to originate from the cubital basivenale (Kukalová-Peck 1978).

All flight-adapted wings require an asymmetrical blade with a strong anterior (costal) margin. This was achieved by the fusion of PC, CA, CP and ScA. These veins are still separated from each other basally in many fossils, but were brought together by fusion in most Recent wings. Primitively, the PC was formed as a smooth or serrated

strip; in more derived wings this strip has either widened into an epipleuron (as in beetles) or vanished. Apart from this, there has never been a precostal area of the wing (the so-called 'precostal' area of orthopteroids is a misinterpretation, see Fig. 6.18). Changes in AA and AP in the anal area of the fore and hind wing provide important, largely untapped evidence for relations among orders. The wing membrane originally bore an archdictyon (meshwork of polygonal cells), later reduced to cross-veins or clear membrane. Secondary veinal elements, small branches, net-like formations, cross-veins, struts (such as the erroneously interpreted 'M₅') and intercalated sectors, are frequently re-formed from membrane. Wing folds (medial, claval, anal and jugal) are important landmarks, but their courses (especially that of the medial fold) sometimes vary.

According to biomechanical calculations, braces are essential in flapping wings to make them flight-worthy. To form a brace, a vein connects with another vein by a strut (cross-vein), or two veins may fuse directly over a short or long distance. An anal brace, preventing the anal area from buckling, is essential for flight and is present in all flying wings. It is achieved either by sclerotisation of the anal membrane basally (the most primitive condition; seen in most palaeodictyopteroids), or by diverse fusions between AA and Cu (derived three times: in Permian themistida, in Ephemeroptera + odonatoids, and in Neoptera). Other braces (especially between MP and CuA) are often but not always present and are formed by various means. The deformability of wings was studied by Wootton (1981a).

Recent advances in the study of the origin of wings and flight were summarised by Kukalová-Peck (1983, 1987), Wootton (1986) and Wootton and Ellington (in press). Evidence from several biological disciplines and the fossil record indicates that the insect wing evolved from a movable appendage, possibly a flattened exite, of the first leg segment (Kukalová-Peck 1983, 1985, 1987). An alternative exite-plus-endite model was proposed by Trueman (1990). A variety of hypotheses have been offered to explain the adaptational events that may have led to the origin of wings. Most of those based on aerodynamic considerations face the difficulty of explaining the adaptive value of winglets during transitional stages. Alternative hypotheses involve preadaptation of organs evolved for a different purpose, namely thermoregulation (Kingsolver and Koehl 1985, 1989) or gill ventilation and swimming (Kukalová-Peck 1983, 1985, 1987).

During the development of immature insects, tracheae grow secondarily into the blood lacunae of the wings. The pattern of these tracheae is often (but not always) conservative and helpful in homologising the veinal system. Later in development the cuticle forming the blood lacunae hardens into wing veins. In extinct forms, this hardening already occurred in nymphs.

It will be demonstrated in the following account of fossil history that pterygote venation can be homologised, based on the complete groundplan outlined above. However, most previous and current descriptive works on wing venation (e.g. Wootton 1979) employ vein notations

reflecting groundplan reconstructions in which the venations are simpler and do not include all homologisable primary veins; such notations occur elsewhere in this book (see Chapter 1 and Table 17.1).

Groundplans of Pregenital Segments and Genitalia

A schematic reconstruction of a pregenital abdominal segment (Fig. 6.3B), integrating all appendages observed on fossil and extant insects, shows the pterygote abdominal pleuron, the arrangement of exites and endites and the primitive triangular sternum (occurring in Archaeognatha and Endopterygota). The highest number of abdominal leg-derived appendages on one abdominal segment is 8. Epicoxal exites (winglets, plate gills) are serially homologous with wings, and in Recent ephemeropteran nymphs they are attached to the same series of leg muscles and interneurons as are the thoracic wings. In all Palaeozoic ephemeropteran nymphs, winglets occur together with leglets on 9 abdominal segments; therefore, plate gills cannot be flattened leglets. In Neoptera, epicoxal exites occur rarely in nymphs (Fig. 6.17B) and adults (e.g. Carboniferous *Eucaenidae*). A complete set (two pairs) of coxal and trochanteral endites (vesicles) on abdominal segments 1–7 were found in Carboniferous *Thysanura* (Fig. 6.9F) (Kukalová-Peck 1987) and Archaeognatha (Kukalová-Peck unpubl.). The pleuropodia of modern endopterygote embryos occur between rudiments of leglets, and appear to be homologous with trochanteral endites.

The leg segments comprising the hexapod genitalia were identified by E. L. Smith (1969, 1988a) and the ancestral conditions for the possible groundplan were proposed by Kukalová-Peck (1987). Pterygote male genitalia on segment 9 consist of a coxopodite (fused SCX, CX and TR) projecting dorsally to form a narrow, medially fused bridge (mesocoxite, MCX, Fig. 6.10D); ?CX endites forming the transversely annulated gonapophyses; and the ?TR endites forming the superimposed, ducted, obliquely annulated penes. These endites articulate with the coxopodites under the mesocoxite. The free gonostyli (claspers) are composed of PFE (with exite), FE, PAT, TI, BT, subsegmented TA, and PT ending in double claws (Figs 6.10B, G, 13D). In the Permian Ephemeroptera, small gonostyli, gonapophyses and penes were found also on segment 8, in addition to epicoxal exites (plate gills) on 8 and 9.

The female genitalia of Dicondylia (*Monura*, *Thysanura*, *Pterygota*) (Figs 6.9A, B, F, 10C, E) have a pronounced gonangulum (SCX9 fused with S9 and intersternite 8-9) as an apomorphy. The gonangulum is not formed in Monocondylia (Archaeognatha), in which SCX9 is a free podite resembling the maxillary cardines. The gonangulum is adjacent or attached to T9 and provides a firm base or a fulcrum, against which the coxo-trochanter 9 (gonocoxite) may rock back-and-forth. Coxo-trochanter 8 bears an articulated TR endite serving as the 1st valve. Coxo-trochanter 9 also bears an articulated TR endite, which forms the 2nd valve and slides in a tongue-and-groove fashion against the 1st valve. As the coxo-trochanter 9 rocks against the gonangulum, the 2nd

valve moves with the 1st valve (or independently by means of its own musculature). The free leg of segment 9 (gonostylus; PFE–PT, ending in double claws) is articulated to coxo-trochanter 9 and may have originally steadied the ovipositor. Later, gonostyli 9 may interlock with the valves 9 to form a 3rd valve. The gonocoxite may become posteroventrally elongated to protect the valves. The female genitalia retained only trochanteral endites on which the original annulations became the teeth or ridges of the cutting surfaces. Almost all Palaeozoic pterygotes have these cutting ridges, suggesting that they oviposited into slits in plant stems.

Cerci

The cerci of Insecta (including *Diplura*) articulate with a characteristic, complex condyle composed of tergum, sternum and coxopodite (SCX, CX and TR) of segment 11, all fused together, while the cerci of *Parainsecta* (*Protura*) articulate with the coxopodite alone. This complex cercal base is undivided in Archaeognatha but secondarily divided into two parts in *Thysanura* and *Pterygota* (*Cercofilata*). Cerci evolved from functional (pushing) leglets (PFE–PT) of segment 11. Cercal leglets are preserved only in Palaeozoic *Monura* (Fig. 6.9A), and had the same segmentation as abdominal leglets and gonostyli. Annulated, filamentous cerci evolved at least 3 times (in *Diplura*, Archaeognatha and *Cercofilata*) (Kukalová-Peck 1987; E. L. Smith unpubl.). The caudal prong (elongated segment 12) in *Protura* is a primitive feature, which was transformed into an annulated caudal filament in Archaeognatha, *Monura*, *Thysanura* and Ephemeroptera.

Metamorphosis

All Recent *Pterygota*, holometabolous as well as hemimetabolous, undergo metamorphosis and have one, two or several metamorphic instars. During metamorphosis, the size of the wings increases dramatically and the wing articulation is formed. All Recent nymphs have their wing pads firmly fused with the terga, but a few (e.g. the nymphs of some *Plecoptera* and of peloridiid *Hemiptera*) retain vague remnants of articular sclerites or have the wings still separated from the terga by sutures. Residual, preadult wing movement is retained in the nymphs of dragonflies and grasshoppers, which change orientation of the wing pads during late ecdysis. The subimagos of mayflies still can fly.

In contrast to this, in Palaeozoic Palaeoptera, Ephemeroptera (Figs 6.4, 14D, F), Protodonata (Fig. 6.15H) and all palaeodictyopteroids (Figs 6.5, 10G, 12C, 13B, C) as well as ancestral plecopteroids (Fig. 6.17B), ancestral hemipteroids (Fig. 6.6), and possibly other groups, immature wings are articulated and the articular sclerites surround the wing base like a horseshoe (as is still indicated in Recent *Plecoptera* nymphs) (Kukalová-Peck 1985). Primitively in pterygote insects, development was gradual without interruption by a metamorphic moult, older nymphs very probably could fly, and there were several flying subimaginal instars. Immatures of some other U. Palaeozoic groups, such as stem-group blattoids, had their wing pads already fused with the terga

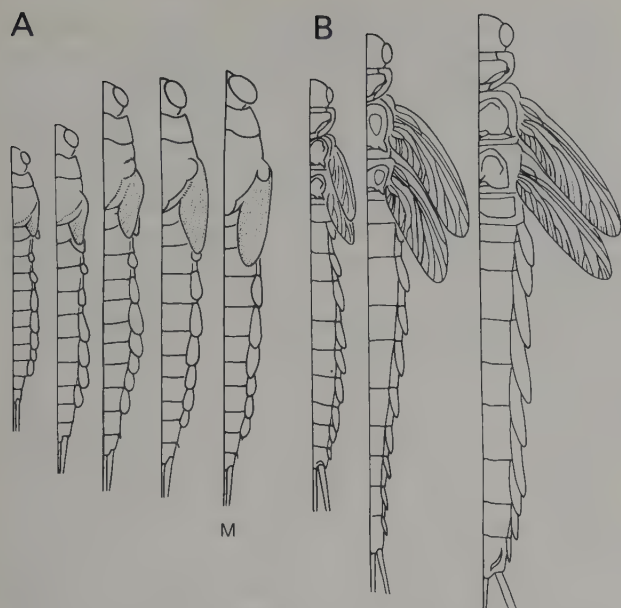


Fig. 6.4 Development in Ephemeroptera: A, Recent mayfly nymphs (Siphonuridae) with fused wing pads and with metamorphic instar (M); B, Permian Kukaloviidae with articulated, movable, gradually developing wing pads and no metamorphic instar. [After Kukalová-Peck 1978]

but sometimes still separated from terga by a suture (Figs 6.19E, F). They required a metamorphic moult to develop into an adult with fully articulated wings.

The young nymphs of some Palaeozoic insects had wing pads attached to the terga by membrane, without visible articular sclerites, whereas older nymphs of the same species possessed well-articulated, movable wing pads (Rasnitsyn 1981; Kukalová-Peck 1983). This suggests that in some nymphal wings the development of an articulation was delayed until the later instars. Later, the articulation and development of the wings were suppressed also in later instars; and eventually the suppression became so advanced that a metamorphic instar became a necessity, in order to restore the wings to their original functional condition.

Clues from the fossil record show that metamorphosis was absent in some extinct orders and evolved independently, in parallel and at different rates, in all modern lineages: ephemeropterans, odonatoids, plecopteroids, orthopteroids, blattoids, hemipteroids and endopterygotes (Kukalová-Peck 1978, 1983, 1985).

Palaeozoic Palaeoptera with permanently (secondarily) outstretched wings (Ephemeroptera, Protodonata, most palaeodictyopteroids) had the following peculiar development (Figs 6.4, 5, 12B, C, 13A–C): the wings in young nymphs were arched backwards; the arch (nymphal wing bend) straightened a little in each subsequent instar, until the wings were fully outstretched. In the absence of a metamorphic moult, this required many nymphal and subimaginal instars. Articulation and sclerotised wing venation were present, even primitively in the young nymphs.

Externally developing, functionally (laterally) posi-

tioned wing buds (Fig. 6.2B) require protection and prevent juveniles, with small wings and presumably imperfect flight, from hiding and moving in confined spaces. In some Palaeozoic juveniles the wing buds were already suppressed, allowing the animals to occupy interstitial habitats where they could hide from predators. The development of adult features was confined largely to one or two instars, the metamorphic instars. The selective advantage of this strategy is indicated by the almost total extinction by the end of the Permian of winged insects which did not have some form of metamorphic instar.

Metamorphic instars are best developed in the endopterygotes. In this group, early juvenile instars (larvae) are very unlike the adults and the metamorphic instars are known as prepupae and pupae. Unencumbered by external, developing adult features, larvae have been able to burrow, hide and exploit many habitats and food sources unavailable to their corresponding adults. Often larvae feed in concealed or conveniently humid microhabitats and require less sclerotisation than do adults. Delayed sclerotisation of larvae and invagination of the wing anlagen into pockets were the major early achievements of endopterygotes.

The oldest known fossil larva (Fig. 6.26A) is soft bodied, polypodous and eruciform, with a segmented head bearing ocelli, a dicondylous mandible probably with *kinetodontium* ('lacinia mobilis', a movable spine) (symplesiomorphy with Crustacea), leg-like palps, segmented thoracic legs and abdominal leglets (all with dou-

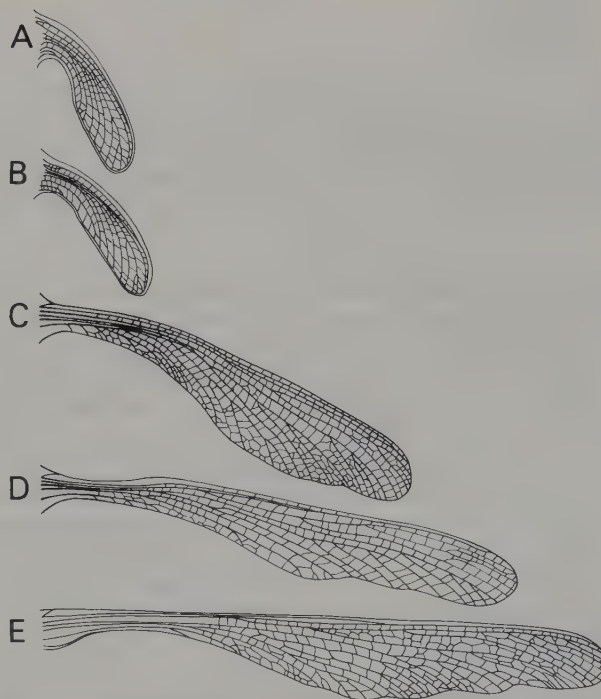


Fig. 6.5 Development in Megaseoptera. A, B *Mischoptera*, nymph; C, *Cauloptera*, subimago; D, *Arcioneura*, subimago; E, *Arcioneura*, adult. Confluent wing development in Megaseoptera by gradual straightening of nymphal wing bend; metamorphic instar lacking.

[A, B after Carpenter and Richardson 1968;
C–E after Kukalová-Peck 1975b]

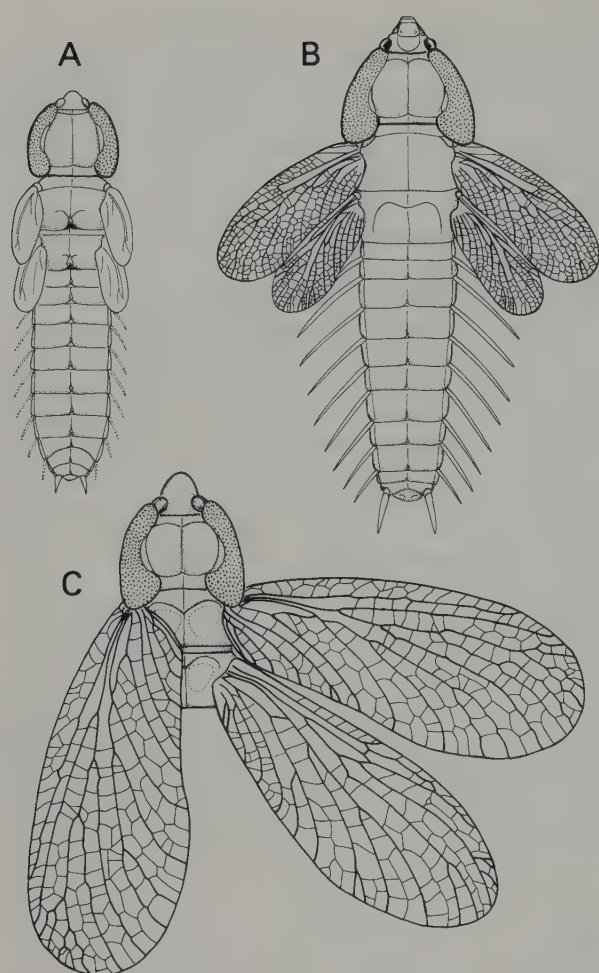


Fig. 6.6 Development in Neoptera nymphs with movable wings: *Herdina mirificus*, hemipteroid assemblage, Herdiniidae, U. Carboniferous of Illinois, U.S.A.: A, B, nymphs; C, adult. Confluent wing development without metamorphic instar; nymphs had fully articulated wings often preserved at different angles. [J. Kukalová-Peck]

ble claws); the antennae were moderately long and annulated, and the cerci short and annulated. This larva lived in a tropical, U. Carboniferous swamp and was close to the mecopterid-hymenopterid type but also resembled a nymph (Kukalová-Peck 1988a). It has been suggested that the pupa evolved as a response to a seasonally cold or dry climate. However, the occurrence of these very primitive Carboniferous larvae in an environment that lacked seasonal extremes argues against this. Alternatively, the pupa, whose original function was to retrieve wings and other suppressed structures, may represent a preadaptation which enabled some, specialised endopterygotes to survive unfavourable climatic periods.

Palaeozoic nymphs and larvae are polypodous. Abdominal leglets and coxal and trochanteral endites are retained in some Recent embryos (Megaloptera, Mecoptera) as a symplesiomorphy. Megalopteran larvae have abdominal filaments (leglets) as gills and coxal endites as gill tufts. Some eruciform larvae use abdominal leglets (prolegs) for walking and coxal endites of segment 11

(pygopods) for pushing. Leglets or other leg-derived abdominal appendages sometimes reappear as rudiments in highly derived, worm-like, Recent larvae (e.g. 'secondary prolegs' of dipterous larvae; see Fig. 39.13D). Fossils show that the oldest endopterygote larvae were derived from nymphs and have similar head and appendages. They are by origin not neotenic (i.e. homologous with the embryos of non-endopterygotes). If they were, Recent larvae would contain only undifferentiated morphogenetic fields forming the wing anlagen at metamorphosis. Instead, some larvae, even at hatching, possess distinguishable wing anlagen and imaginal discs (Wigglesworth 1972).

Palaeozoic developmental series were very gradual, with numerous nymphal and subimaginal instars, but modern series are much shorter. Probably, several subimaginal instars were condensed into the adult stage (causing postponement of sexual maturity), the rest of subimaginal and older nymphal instars formed one or several metamorphic instars (frequently two, prepupa and pupa), and the younger instars compressed into fewer, composite nymphal instars. The pattern of condensations and compactions may have varied from one insect lineage to the next, but the overall trend to fewer moults was the same in all lineages. Insects are very vulnerable during moulting episodes, so it was an advantage to them to reduce the number of these required to complete development (Kukalová-Peck 1978, 1983, 1985).

Metamorphosis, which is defined by the presence of a metamorphic instar, occurs only in Pterygota (but not in all orders). In primitively wingless insects (Archaeognatha, Monura and Thysanura) it was never developed. Several extinct pterygote orders and some direct ancestors of living families (e.g. in Ephemeroptera) developed without a metamorphic instar. The Hemimetabola are not a natural group. The Holometabola (= Endopterygota) are monophyletic and are best defined by the invagination of wing buds, since the pupa is the consequence, not the instigation, of endopterygoty (Kukalová-Peck 1978, 1983, 1985, 1987).

HISTORY OF THE ORDERS

A phylogeny of the major hexapod lineages as indicated by characters visible in fossils and by homologised wing venation is given in Fig. 6.7, and the occurrence of these groups in the fossil record is shown in Table 6.1.

HEXAPODA

(Devonian–Recent). Hexapoda share with their sister group, the Myriapoda, the presence of Malpighian tubules, Tömösvary organs and a subdivided tentorium, the loss of the mandibular palp, and the location of the head appendages of segment 3 (the equivalent of the second antennae in Crustacea) inside the oral cavity (all synapomorphies). In their groundplan hexapods have 3 pairs of longer thoracic legs, bearing up to 5 exites and a coxal endite; thoracic legs with a fused patello-tibia, a tarsus with 2 subsegments and a pretarsus with 2 claws (ungues); a thoracic pleuron (SCX spread flat) primitively

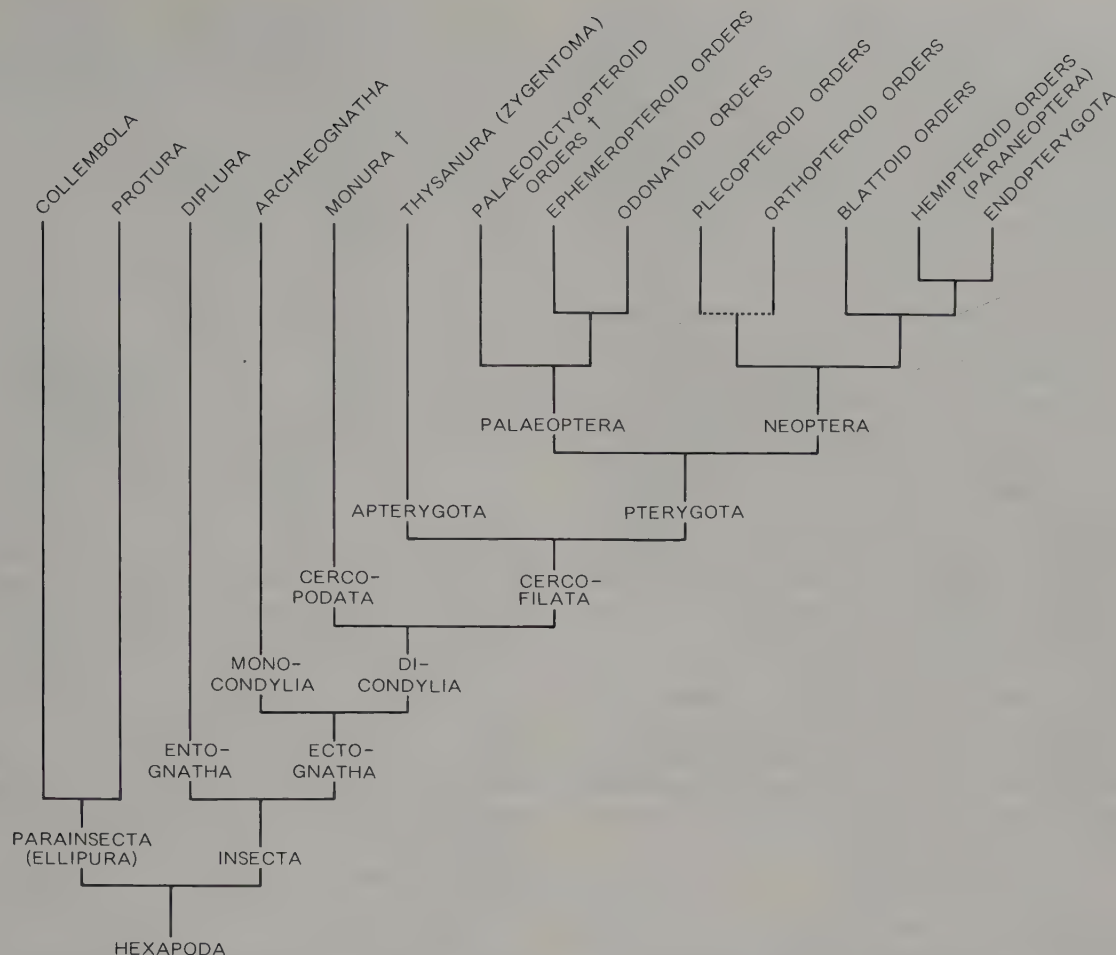


Fig. 6.7 Phylogeny of the major groups of Hexapoda as indicated by features visible in fossils and by newly homologised wing venation.

absent (but present in all Myriapoda possibly as an apomorphy); shorter abdominal leglets, each with a fully articulated patella, on all abdominal segments except 10; a pair of exites (ECX) and 2 pairs of endites (CX and TR) on each of 9 abdominal segments; a coxal endite on segment 11; a caudal prong on abdominal segment 12; an abdominal pleuron composed of 1–3 flattened leg segments (SCX but also incorporating CX and TR in derived condition); head and genital appendages each with 2 pairs of leg endites (CX and TR) transformed into working parts; and fused leg segments (SCX + CX + TR + 2 endites) forming a mandible (Figs 6.2, 3A, B, 9B–D) (SCX and CX separate and 2 endites aggregated with TR in Myriapoda). [Kukalová-Peck 1987; E. L. Smith unpubl.]

PARAINSECTA (= ELLIPURA)

(Devonian–Recent). Probably the sister group of Insecta. Primitive features include an abdominal pleuron incorporating SCX only (CX and TR on the abdomen are separate podites not combined into SCX + CX + TR as in Insecta, except on segment 9); presence of eyes on head segments 2–3 (as in Myriapoda); antennae not flagellar, formed by 6 true leg segments with extrinsic leg musculature; presence of post-antennal or Tömösvary's organs (as in Myriapoda); cerci borne on a free cox-

opodite (SCX + CX + TR); and anamorphic development (with segments added to the abdomen after hatching from the egg). Apomorphies include the enclosure of the mouth-parts between the labium and sidelobes (ECX) of the head (entognathy); an immobile clypeolabrum and labium; incorporation of the maxillolabial diplosomite into the cranium; loss of the movable spine (kinetodontium or 'lacinia mobilis') on the mandible; vestigial palps; reduced prothorax; fragmentation of the thoracic SCX into pleural annuli; extensive fusion of segments and loss of exites and double claws in the thoracic leg; abdominal leglets heteronomous, never complete and without TR endites; and cerci stylar. The group also possesses a unique type of sperm cell, differing from that found in true insects (Omodeo *et al.* 1980). Parainsecta contains the sister groups Collembola and Protura, the latter being characterised by a number of reductions. [Kukalová-Peck 1987; E. L. Smith unpubl.]

Collembola (Devonian–Recent). Neotenic; derived from early anamorphic forms; compound eyes (of dispersed facet type) placed on head segment 2–3; 4 ocelli present. *Rhyniella praecursor* from the base of the L. Devonian of Scotland is a derived collembolan with fully enclosed mouth-parts, and resembles Isotomidae. A possible member of the Neanuridae and additional specimens

are known (Greenslade and Whalley 1986; Greenslade 1988). Early Collembola were semi-aquatic. Entomobryidae lived in the L. Permian of South Africa (Riek 1976a), and *Protentomobrya* in the U. Cretaceous of Canada. Several Recent genera are represented in Eocene Baltic amber. Oligocene Dominican amber contains Isotomidae, Entomobryidae and Sminthuridae, all but one with Recent genera. Miocene amber from Chiapas, Mexico has a similar fauna.

INSECTA*

(Devonian–Recent). Hexapoda with the following apomorphies: abdominal pleuron coxopodite-like, composed of SCX, CX and TR; antennae flagellar, annulated, without extrinsic leg musculature; anterior ocelli fused together; eyes shifted to head segment 4; larval development epimorphic (all abdominal segments present at hatching). Abdominal leglets 11 (cerci) have a derived, complex base composed of tergosternum 11 and SCX + CX + TR all fused together. Primitive features include a mobile clypeolabrum and labium; maxillolabial diplosomite (5–6) forming a separate tagma; mandibular kinetodontium ('lacinia mobilis') present; palps completely segmented; legs with 2 ungues (claws); prothorax not reduced; thoracic SCX a true, movable leg segment, not flattened into a pleuron and not subdivided or fragmented (in Archaeognatha only); BT and TA separate; tarsus with 2 subsegments; and abdominal leglets fully segmented with 8 joints. [Kukalová-Peck 1987]

ENTOGNATHA

(Carboniferous–Recent). Diplura (Fig. 6.8) only. Cryptic insects with the following apomorphies: largely reduced appendages (still fully segmented in fossils); mouth-parts protrusible, enclosed in cavity formed by fusion of labium with sidelobes of head (still widely opened in fossils); archilabrum enlarged; thoracic SCX (pleuron) fragmented into 2–3 annuli; cerci flagellar with complex insectan base (Kukalová-Peck 1987; E. L. Smith unpubl.). Segmented abdominal leglets of Carboniferous Diplura show that the abdominal pleuron contained three leg segments, the antennae were flagellar and the cercal base was composed of fused tergum, sternum and coxopodite 11, all as in Ectognatha. The structure of the sperm cell in Diplura is also similar to that in Ectognatha (Omodeo *et al.* 1980). The thorax of modern Japygidae shares all the basic muscles with Archaeognatha and Thysanura and some with Pterygota (Barlet and Carpentier 1962). Numerous thoracic features indicate a common ground-plan with Ectognatha, not with Parainsecta (Barlet 1988). Both CX and TR vesicles are present in living Diplura, but the latter are more prevalent. The U. Carboniferous *Testajapyx* from Illinois (Fig. 6.8) was an active predator with faceted eyes and relatively long and fully segmented appendages (palps, thoracic legs and abdominal legs), as in Ectognatha. *Onychojapyx* was found in the Miocene-Pliocene of Arizona (U.S.A.).

* This term is usually used in a more restricted sense to exclude the Diplura (see Chapter 5).

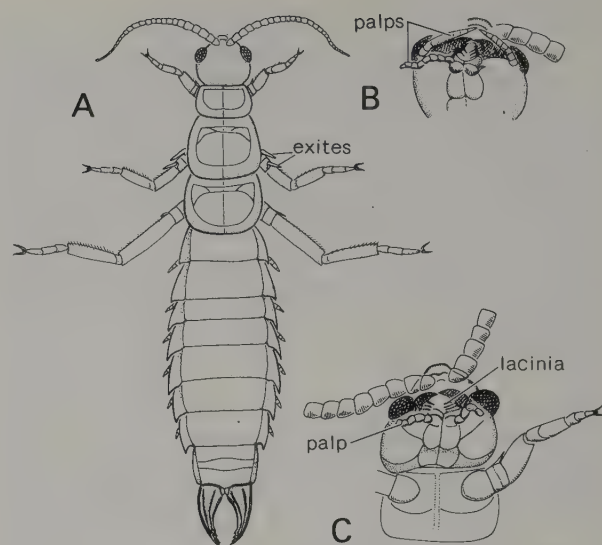


Fig. 6.8 Entognatha: Diplura. A, *Testajapyx thomasi*, U. Carboniferous of Illinois, U.S.A., dorsal; B, C, same, head, ventral, with fully segmented palps and comb-like lacinia. Entognathy is only partly developed.

[After Kukalová-Peck 1987]

ECTOGNATHA (= INSECTA)

(Devonian–Recent). Free-living insects with external mouth-parts articulated by SCX and with many mobile, leg-derived appendages, exites and endites, moved by leg muscles, CX endites being equally or more prevalent than TR endites. In Monocondylia (Archaeognatha), the meso- and metathoracic pleura are not yet formed (SCX remains a recognisable leg segment), the gonangulum is absent, the mandibles are narrow with a single, posterior articulation, and the cercal bases are complex but undivided (all primitive features). In Dicondylia (i.e. the rest of the insects), the thoracic pleuron is formed by SCX spread flat, the gonangulum is present, and the mandibles extend anteriorly creating a secondary condyle with clypeotenotrium (all apomorphies). Primitively the anterior condyle is shaped like a paired socket, later reduced to a single (outer) socket which can be expanded into a slide, and the articulation is voluntary (i.e. can be disconnected at will). A permanent anterior condyle, based on a single outer socket, is the derived condition, and this has been achieved independently in Neoptera and the odonatoid assemblage. An isolated, dicondylous mandible (named as *Rhyniognatha hirsti*) from the base of the L. Devonian in Scotland belongs to the Dicondylia (Hennig 1981).

Archaeognatha (L. Devonian–Recent). Bristletails are the only representatives of the Monocondylia. They have a number of primitive features, such as the retention of segmental sutures on the monocondylous mandibles, a fully segmented maxillary palp (leglet) with two claws, the presence in the meso- and metathorax of an independent, ring-like SCX (which is not flattened and transformed into a pleural wall support), undivided cercal bases, abdominal rope muscles, and an ovipositor with SCX9 not associated with the tergum, e.g. lacking a gonangulum. The abdominal rope muscles, which are

shared with Crustacea and probably Monura, are used in escape jumps and triggered by special sensory bristles. Apomorphies include the loss of the mandibular kinetodontium, reduction of PFE in the labial palp and its incorporation into the labium, and annulated cerci. Fragments of well advanced machilids are known from the L. Devonian of Quebec (Labandeira *et al.* 1988) and M. Devonian of Gilboa, New York (Shear *et al.* 1984). Archaeognatha misinterpreted as 'Monura' occur in the U. Carboniferous of Illinois. They had narrow mandibles and cranial sidelobes, maxillary palps with double claws, very short cerci with only 3 annuli, narrow thoracic sidelobes separated by sutures and distinctly segmented abdominal leglets; some bore heavy spines, and CX and TR endites-vesicles were on all pregenital segments (Kukalová-Peck unpubl.). *Triassomachilis* from the Ural Mts is a mayfly nymph. Eocene Baltic amber contains living archaeognath genera (Stach 1972).

Monura (U. Carboniferous–Permian). Monura (Figs 6.9A–C) superficially resembled machilids and were the only insects retaining cercal legs. They form the sister group (Cercopodata) of the Thysanura + Pterygota (Cercofilata) (Fig. 6.7). Primitive features of the Monura included the segmented head (but without cranial sidelobes); the non-permanent, anterior condyle on a broad mandible; the fully segmented maxillary and labial palps (but with a single pretarsal claw); the fully segmented abdominal leglets (PFE–PT) which end in double claws;

the long caudal filament; and the body covering of sensory bristles. The dicondylous mandible, gonangulum and well sclerotised thoracic pleuron are synapomorphies with Thysanura + Pterygota, but the thoracic pleuron lacks the reinforcing pleural sulcus characterising that group. Thoracic sidelobes were protruding laterally and were fused with the terga but separated from them by deep sutures; the cercal bases may have been undivided as in Archaeognatha (Kukalová-Peck 1985, 1987). *Dasyleptus* (Fig. 6.9A) probably climbed on emergent swamp vegetation and jumped away for safety, even from water surfaces, as do Recent machilids. Cast cuticles of Monura occur frequently in the U. Carboniferous of the U.S.A. and France, and in the U. Permian of the U.S.S.R.

Thysanura (Zygentoma) (U. Carboniferous–Recent). Silverfish are the sister group of Pterygota, with which they share a divided cercal articulation, a dicondylous mandible and a pleural sulcus in each thoracic pleuron (in Thysanura a reduced sulcus is noticeable in fossils only) (all synapomorphies). The mandibles can be rocked by means of two sockets which fit into a clypeotentorial yoke (the most primitive non-permanent anterior condyle). The head is segmented. The thoracic pleura (= SCX spread flat) became partially desclerotised forming crescents to which leg muscles are attached; this apomorphic pleuron is characteristic of Thysanura and correlated with leg movements. Proto-wings and epicoxae were transformed into thoracic sidelobes, but retained tracheae

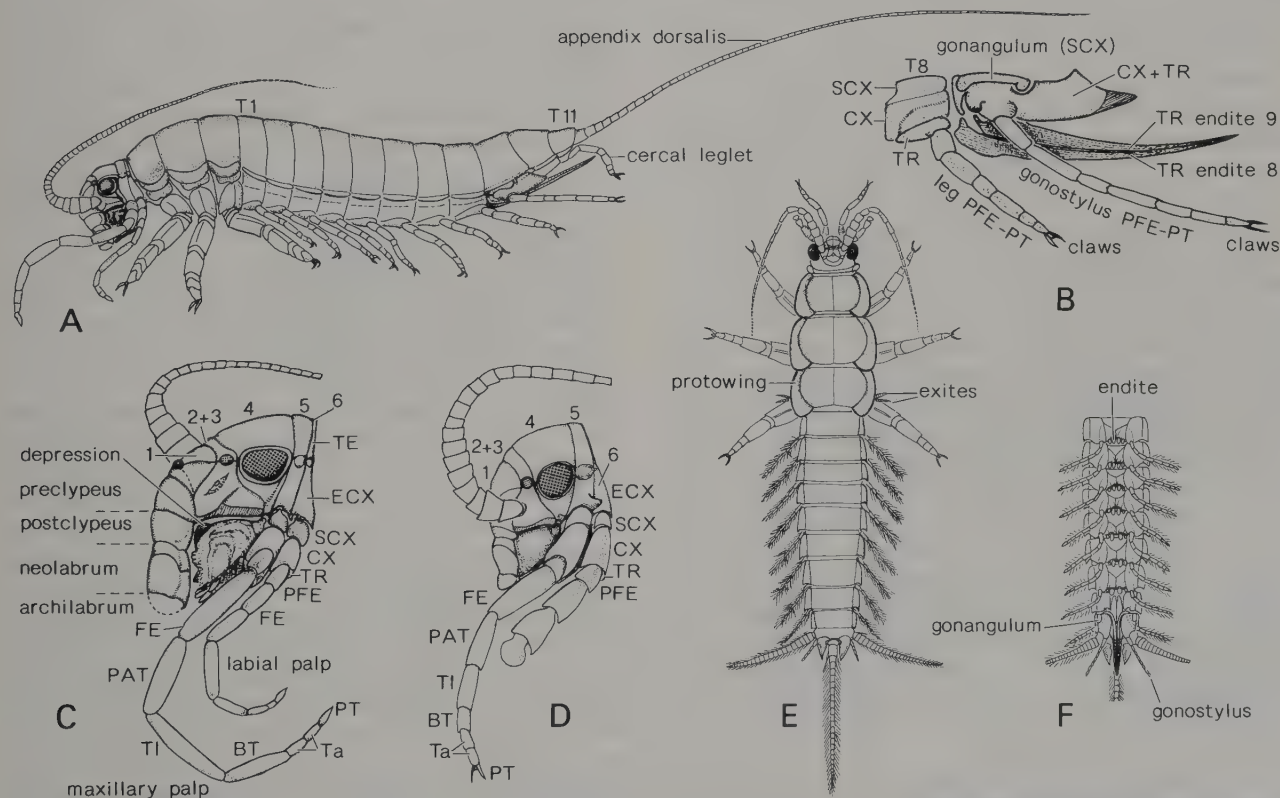


Fig. 6.9 Cercopodata: Monura: A–C, *Dasyleptus* sp., U. Carboniferous of Illinois, U.S.A.: A, adult female, lateral, with cercal leglets instead of cerci; B, ovipositor, close to groundplan of Dicondylia; C, segmented head. All abdominal legs, gonostyli and cercal leglets have claws. Thysanura: D–F, *Ramsdelepidion schusteri*, U. Carboniferous of Illinois, U.S.A.: D, segmented head, lateral; E, female, dorsal, with segmented head, thoracic side-lobes (homologous to proto-wings), and 2 pairs of abdominal vesicles (endites) on first 7 segments; F, abdomen, ventral. Lettering as in Fig. 6.1.

[After Kukalová-Peck 1987]

branched as in ephemeropteran nymphal wings. The gigantic *Ramsdelepidion schusteri* (body length 60 mm) from the U. Carboniferous of Illinois (Fig. 6.9D–F) had all sidelobes still separated by sutures, a full set of long, abdominal, segmented leglets with sensory bristles, and two pairs of endites serving as vesicles on all pregenital abdominal segments, including the first (all primitive features) (Kukalová-Peck 1987, 1988b).

PTERYGOTA

(?L. Devonian–Recent). The sister group of the Thysanura, Pterygota owe their biological success to wings. Morphological studies of Palaeozoic hexapods, embryology, genetics, transplant experiments, development and neurophysiology (Kukalová-Peck 1983, 1987), all indicate that wings evolved from articulated, leg-derived and originally mobile proto-wings. The same evidence indicates that proto-wings were derived from appendages of legs, possibly from the first epicoxal exites, and the wing articulation from the first leg segment (ECX). Proto-wings were flattened and subdivided into densely dichotomously branched cuticular ridges for flexibility and blood distribution, as are telson plates in Crustacea. These ridges evolved later into 8 dichotomously branched venational pairs. The groundplan venation was regularly but weakly fluted and veinal ridges were expressed in both dorsal and ventral wing membranes. Proto-wings probably served as respiratory, ventilatory and later as locomotory devices, presumably first in aquatic or amphibious conditions.

All major, extant, pterygote assemblages (ephemeropterans, odonatoids, plecopteroids, orthopteroids, blattoids, hemipteroids and endopterygotes) occur in the Carboniferous, and all show, even at this time, their own special adaptation of the proto-wing groundplan venation. A special type of divided cercal articulation, flagellar cerci, dicondylous mandibles, a gonangulum and an invaginated sulcus in each thoracic pleuron are features shared with Thysanura (*Zygentoma*). The thoracic pleural sulcus, basalare and subalare are used as wing pivots. In primitive fossil pterygotes, each thoracic leg bore at most one (coxal) endite (in Plecoptera and some neuropterids) and up to 4 exites. Each abdominal segment, except 10, bore at most 8 leg-derived appendages: 2 epicoxal exites, 2 leglets (sometimes forming gonostyli or claspers), 2 coxal endites (forming vesicles or male gonapophyses) and 2 trochanteral endites (forming vesicles, male penes or female ovipositor valves 1 and 2). All 8 appendages are rarely present on any one segment (other than on segments 8 and 9 in an older nymph of a Palaeozoic male mayfly). Exites, leglets and endites are present on up to 9 segments; cerci have coxal endites (in larvae only). Abdominal sterna were originally triangular (Figs 6.3A, B), and this condition is still preserved in Endopterygota. [Kukalová-Peck 1987, 1988b]

PALAEOPTERA

(U. Carboniferous–Recent). Palaeoptera are the sister group of Neoptera and differ from them in having the following apomorphies: M always with a basal stem; veins

strongly fluted and veinal ridges expressed mostly in only one membrane (dorsal or ventral); thoracic coxal endites eliminated; all pregenital, abdominal sterna expanded and their original triangular shape lost; abdominal, pregenital endites and cercal coxal endite completely eliminated; lacinia and galea always fused (Kukalová-Peck 1983, 1985, 1987). The wing articulation consists of numerous, small sclerites densely crowded into a primitive band, which continues under the wing as several basalaria and subalaria (Figs 6.10B, F, 12A–C, 13D, 14E, 15D). In the Diaphanopterodea (Figs 6.10B, F) the articular sclerites remained unfused and the wing could be flexed backwards at rest by a simple mechanism. In all other Palaeoptera various numbers of articular sclerites became fused with each other and with the radial vein, and this enabled the wing to be held permanently outstretched for gliding. Primitive pterygote features retained in the groundplan of Palaeoptera are: band-like wing articulation; veins RA and RP with no common stem; RP and M basally far apart; fully formed, muscled trochantin (a sternal fragment) absent; and abdominal epicoxal exites present (as plate gills). The anterior mandibular articulation in Palaeoptera usually was non-permanent and sliding; only in the predatory odonatoids did it become permanent (a convergence with Neoptera).

Palaeodictyopteroid Assemblage

(U. Carboniferous–Permian). This extinct sister group of the odonatoids + Ephemeroptera includes the orders Diaphanopterodea, Palaeodictyoptera, Megasecoptera and Permothemistida. All had a hypognathous head with a highly domed preclypeus, prominent sucking-piercing mouth-parts forming a rostrum, and specialised, terrestrial nymphs. The rostrum was 0.5–30 mm long and consisted of 5 stylets interlocking by grooves (2 mandibles, 2 lacinio-galeae, 1 hypopharynx) and resting in a labial trough (Fig. 6.10A). Each mandible had two long, sliding, basal articulations. Leg-like maxillary palps and the anteriorly articulated fore legs supported the rostrum during feeding. Large adults and nymphs sucked in entire contents of cones, including spores (Figs 6.10G, 11), while small forms probably imbibed only the juices from ovules. In the wings the rich, dichotomously branched venation and the long, oblique, branched and pronounced CP- and ScA+ were primitive pterygote features. The anal area was braced against buckling by sclerotisation in the basal corner (the most primitive type of anal brace in Pterygota). The prothoracic winglets were articulated and sometimes movable, though probably passively, and had true venation. Nymphs had 3 pairs of articulated wings. Older nymphs could very probably fly (Kukalová-Peck 1983, 1985). Thoracic and abdominal terga and intersegmental membranes of both adults and nymphs sometimes bore numerous, long, thin, hollow, branched, rather stiff projections, textured or covered with hairs and tubercles, which shrouded the body. Up to 4 exites were retained on each thoracic leg, but abdominal exites (plate gills) were fused with ECX sidelobes in terrestrial nymphs. Short abdominal leglets sometimes were present in both

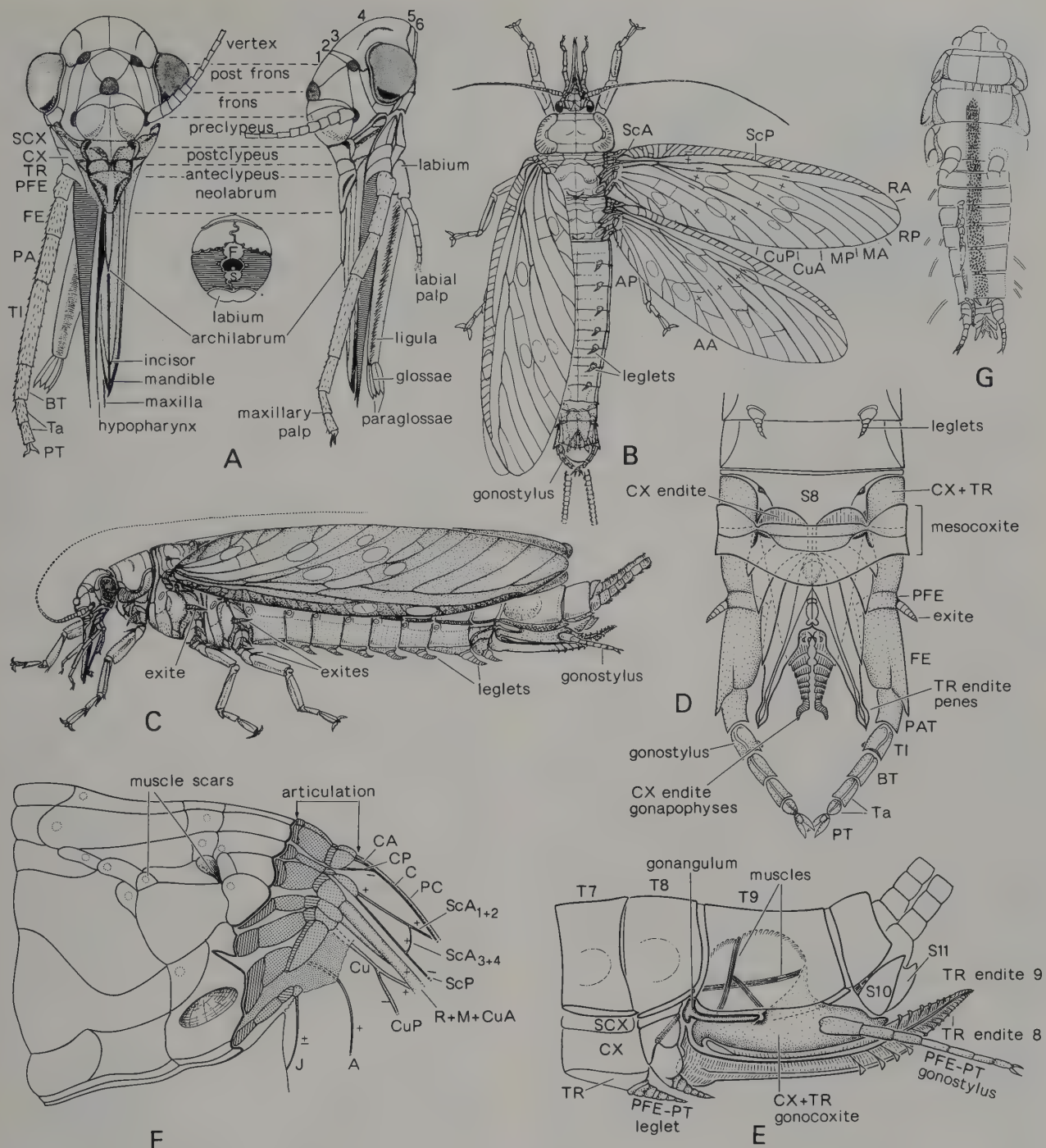


Fig. 6.10 Diaphanopteroidea: A–E, *Uralia rodendorfi*, L. Permian of Ural Mts, U.S.S.R.: A, segmented head, dorsal and lateral, with transverse section of rostrum; F = food canal, S = salivary canal. B, male, dorsal, with ventral structures shown by dotted lines. C, female, lateral, with head in sucking position. D, male genitalia (close to pterygote groundplan), dorsal (tergum removed). E, female genitalia, lateral. F, *Permothymen schucherti*, L. Permian of Kansas, U.S.A., the most primitive wing articulation, showing band-like, unfused sclerites; wing could be flexed back simply by closing gaps and tilting some sclerites (compare with Neoptera, Fig. 6.16). G, nymph (*U. rodendorfi* of Illinois) with wing pads articulated and partly folded and gut filled with spores.

[A, B after Kukalová-Peck 1985; C after Kukalová-Peck 1983; D–F, Kukalová-Peck; G after Kukalová-Peck 1987]

nymphs and adults. There was no metamorphic instar. Palaeodictyopteroids were most diverse in the U. Carboniferous and became extinct at the end of Permian along with most of the primitive Palaeozoic flora.

Diaphanopteroidea (U. Carboniferous–Permian). The

most primitive order close to the base of the assemblage, but with reduced prothoracic wings, specialised gonocoxites and derived, impoverished venation. Medium to small insects with short rostrum (0.5–3 mm) (Figs 6.10A–G) (Kukalová-Peck 1974, 1975a, 1983, 1985). Band-like



Fig. 6.11 Palaeodictyoptera: *Homaloneura lehmani*, U. Carboniferous of France, feeding on a Cordaitales cone. [J. Kukalová]

articulation in the form of a band of sclerites lacking fusions, and very probably close to the pterygote groundplan. Wings flexed by pulling together, crowding and slanting anal and jugal rows of sclerites. Wings were held roof-wise in flexed position in primitive diaphanopterids (Fig. 6.10c), and completely overlapped in some advanced, Permian forms. Long, filamentous dorsal projections and pregenital abdominal leglets present. Thoracic coxae widely separated. Diaphanopteroidea are probably the sister group of Palaeodictyoptera. Genitalia close to pterygote groundplan (Figs 6.10D, E). Gonostyli consist of complete legs with double claws; gonapophyses

and penes retain primitive endite annulation and penes have ducts. Gonangulum fused with tergum; gonocoxite specialised, extended dorsolaterally over valves. Primitive annulation of ovipositor valves forming cutting ridges. PFE associates with FE. Tarsus with 2 subsegments (4 in advanced forms). Nymphs (Fig. 6.10G) shrouded in dorsal projections and capable of pulling their wing pads closer to the body. About 9 families are known from the Northern Hemisphere, mainly from the Permian. Some small Permian forms markedly resemble mosquitoes and might have been feeding on blood (Kukalová-Peck and Brauckmann 1990).

Palaeodictyoptera (U. Carboniferous–Permian). The most common, robust palaeodictyopteroids, with prothoracic wings large, veined and articulated (Figs 6.11, 12A–C); usually large or gigantic, with maximum wingspread of about 56 cm in *Mazonthairos enormis* (Kukalová-Peck and Richardson 1983). Axillary plate small, rectangular, composed of 4–6 sclerites (an apomorphy of the order) (Fig. 6.12A). Hind wings usually triangular and broader than fore wings but sometimes shorter and narrower. Venation primitive, typically richly branched, lacking braces other than ScA+ and with an anal sclerotisation. Colour patterns of wings and body were often intricate and disruptive. Pregenital abdominal leglets and filamentous dorsal projections lost, thoracic coxae widely separated. Ovipositor valves dorsally covered by membranous extension from gonocoxite. Nymphs (Figs 6.12B, C) strongly sclerotised, flattened and sculptured (all derived features within palaeodictyopteroids). Metamorphosis absent. Kukalová-Peck (1969b–70, 1983) reviewed the morphology and phylogeny of the order. There were 21 families, with 71 genera, mainly in the tropics of Northern Hemisphere. Homiopteridae, Homaleneuridae and Dictyoneuridae were the largest families. Psychroptilidae from the U. Carboniferous of Tas. were found in varvitic sediments, indicative of very cold climate (Riek 1976b). Tchirkovaeidae are known from the U. Carboniferous of Siberia (Sinichenkova 1979).

Megasecoptera (U. Carboniferous–Permian). Medium

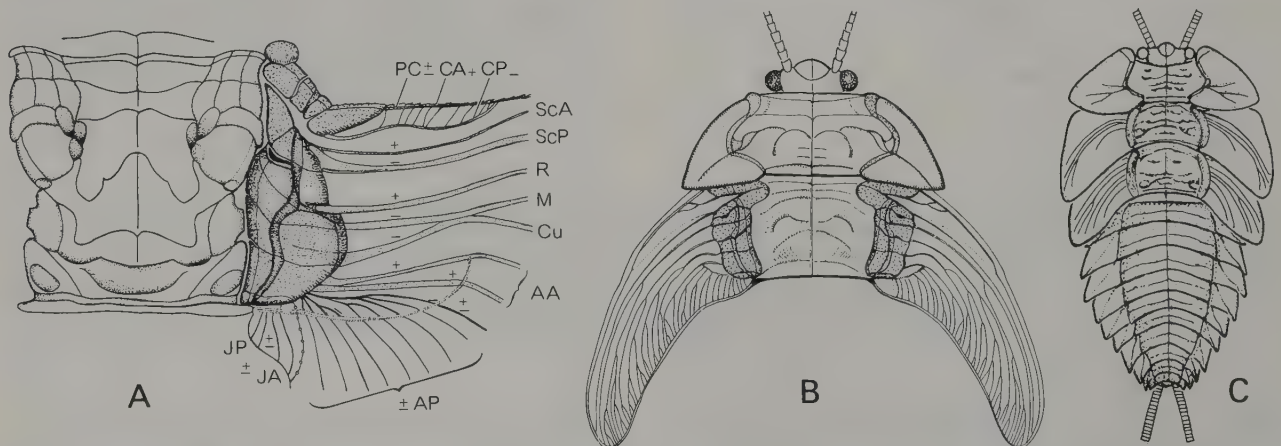


Fig. 6.12 Palaeodictyoptera: A, *Mazonopterus wolfforum*, U. Carboniferous of Illinois, U.S.A., tergum and articular band (stippled) with several sclerites fused to radius, so that wings are permanently outstretched; B, *Adolaryia bairdi*, sclerotised nymph showing articulated pro- and mesothoracic wings; C, *Rochdalia parkeri*, U. Carboniferous of England, 'trilobite' type of armoured nymph. [After Kukalová-Peck and Richardson 1983]

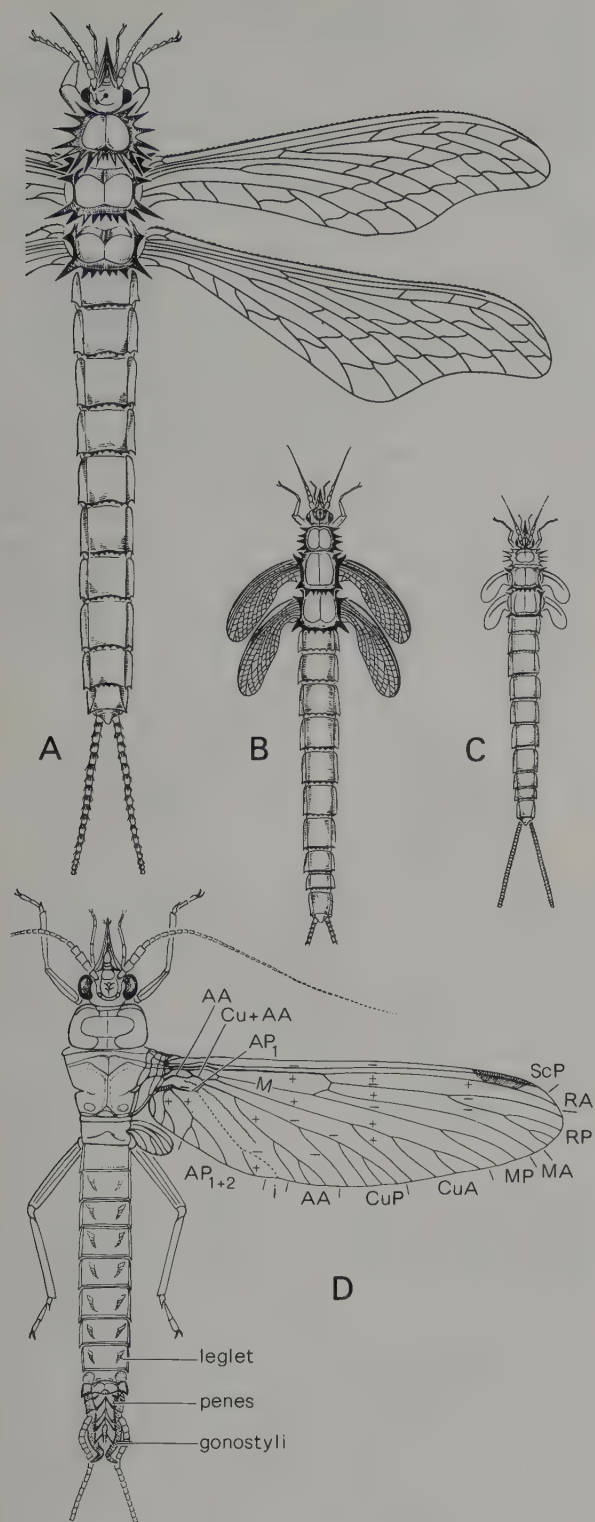


Fig. 6.13 A–C, *Mischoptera* sp., Megasecoptera, U. Carboniferous of France and Illinois, U.S.A.: A, adult; B, nymph; C, young nymph. D, *Diathema tenerum*, Permothemistida, L. Permian of Ural Mts, U.S.S.R., adult with highly reduced hind wings (ventral appendages shown by dotted lines; IA = intercalated anal sector). [J. Kukalová-Peck]

to large palaeodictyopteroids (Figs 6.13A–C) with world-wide distribution, reduced prothoracic wings and genitalia as in Diaphanopterodea. Derived features include homonomous wings with narrow base and simplified, fused and richly braced venation with few branches, and axillary plate long and narrow, composed of many fused sclerites (Kukalová-Peck 1973, 1975b). Rostra were about 3–10 mm long, very broad basally and quickly tapering. Thorax often bulbous; abdomen relatively slim. Thoracic coxae sometimes crowded and sternum between them invaginated to form cryptosternum; this was an adaptation for perching and an autapomorphy. Long, filamentous, dorsal projections and pregenital abdominal leglets present, as in Diaphanopterodea. Nymphs (Figs 6.13B, C) shrouded in long projections, and with functional wings. Metamorphosis absent. There were about 26 families of Megasecoptera in tropical regions. The large Mischopteridae (Fig. 6.13A) had spiny thoraxes and possibly raptorial legs; Hanidae had exceedingly narrow wings; and Eokulojidae had a single pair of wings.

Permothemistida (Permian). Previously known as ‘Archodonata’. Rare, relatively small, with reduced prothoracic wings, very small hind wings, short rostra (ca. 1 mm) and unique venation. Wings with pterostigma and venation with several apomorphic features: very large anal area, convex fold between AA and AP, intercalated sector at AP, fusion near wing base between M + Cu and AA + Cu + CuP. Anal brace double: a palaeodictyopteroid sclerotised bar and a parallel veinal brace of AA to Cu (Fig. 6.13D). Wing articulation can be derived only from that found in Diaphanopterodea. Abdominal leglets present. Male gonostyli and cerci S-curved and penes without duct. Two families, Permothemistidae, known from the Ural region, Arkhangelsk and perhaps Kansas, and Diathemidae from the Urals (Sinichenkova 1980; Riek and Kukalová-Peck 1984).

Ephemeroptera + Odonatoid Assemblage (L. Carboniferous–Recent). These together comprise the sister group of palaeodictyopteroids. Features of the ephemeroptero-odonatoid groundplan include: (1) biting mouth-parts; (2) nymphs aquatic and retaining 9 pairs of leg-derived, abdominal plate gills (serially homologous with thoracic wings) moved by leg muscles (Kukalová-Peck 1983, 1985) and occurring together with 9 pairs of abdominal leglets; (3) adults with complicated, curved, anal brace, unique in Pterygota and composed of several veinal sections; (4) venation with prominent, Y-shaped intercalaries, MA braced shortly with RP, CuA braced shortly with M; (5) RA and RP remaining separate, not basally fused into a radial stem (3 and 4 apomorphic within Palaeoptera).

Ephemeroptera (U. Carboniferous–Recent). Groundplan venation identical with that of primitive odonatoids (Kukalová-Peck 1985), with two exceptions: (1) ScA+ forms prominent arch (apomorphy), and (2) composite anal brace ends on CuP at a bulla (primitive), not at a kink in CuP as in odonatoids (Figs 6.14E, F, 15A). Palaeozoic adult mayflies had functional mouth-parts with sliding mandibular articulations, as seen in modern nymphs, and small, veined, prothoracic winglets; males

had two pairs of gonostyli with double claws on 8 and 9, annulated gonapophyses and penes. Nymphs were aquatic with small prothoracic winglets and 2 pairs of articulated, lateral, mobile wings, 9 pairs of mobile, abdominal winglets (serially homologous with wings but used for swimming and respiration), and 9 pairs of abdominal leglets of which the 9th pair was the longest (Kukalová-Peck 1985; Hubbard and Kukalová-Peck 1980). Metamorphosis absent (Figs 6.4, 14D, F). *Bojophlebia* (Figs 6.14A, B) from the U. Carboniferous of Bohemia reached 45 cm in wingspan, and Syntonopteridae from the U. Carboniferous and Permian of Europe and North America 19 cm. Protereismatidae (Figs 6.14C–F) were widely distributed in the Permian and were probably directly ancestral to Recent subgroups. Plentiful Mesozoic nymphs are mostly of the siphonurid type with large gills, wing pads secondarily firmly fused with terga, and a metamorphic instar. Hexagenitidae dominated in the L. Cretaceous. Mesephemeridae became extinct in the Jurassic. Many Recent subgroups are known since the Jurassic, some since the Tertiary (Chernova 1970; Sinichenkova 1984, 1985, 1986). Siphonuridae (*Promirara*, *Australurus* and *Dulcimanna*) are known from the L. Cretaceous of Vic.

Fossil Leptophlebiidae were reviewed by Hubbard and Savage (1981).

Odonatoid Assemblage (U. Carboniferous–Recent). The odonatoids (Protodonata + Odonata) differ from the Ephemeroptera in having a kink in CuP (synapomorphy of odonatoids) and in lacking the prominent, arched ScA+ which is an apomorphy of Ephemeroptera. The complicated, concavely curved veinal anal brace and groundplan venation is the same as in Ephemeroptera (Riek and Kukalová-Peck 1984). Nymphs have lost the abdominal winglet-gills and use filamentous leglets as gills.

Protodonata (= Meganisoptera) (U. Carboniferous–Triassic). Members of this group (Figs 6.15A–H) reached up to 71 cm in wingspan (*Meganeuropsis americana*, L. Permian, U.S.A.) (Carpenter 1947). The literature is swamped with faulty reconstructions, but new discoveries (Kukalová-Peck unpubl.) indicate the following morphology: head hypognathous (Figs 6.15E–F); powerful mandibles with permanent anterior condyle (apomorphic within Palaeoptera and convergent with Neoptera); prothoracic tergum with narrow lateral margins; pterothoracic terga and wing articulation as in Fig. 6.15D; fore and mid legs long, powerful and articulated far anteriorly;

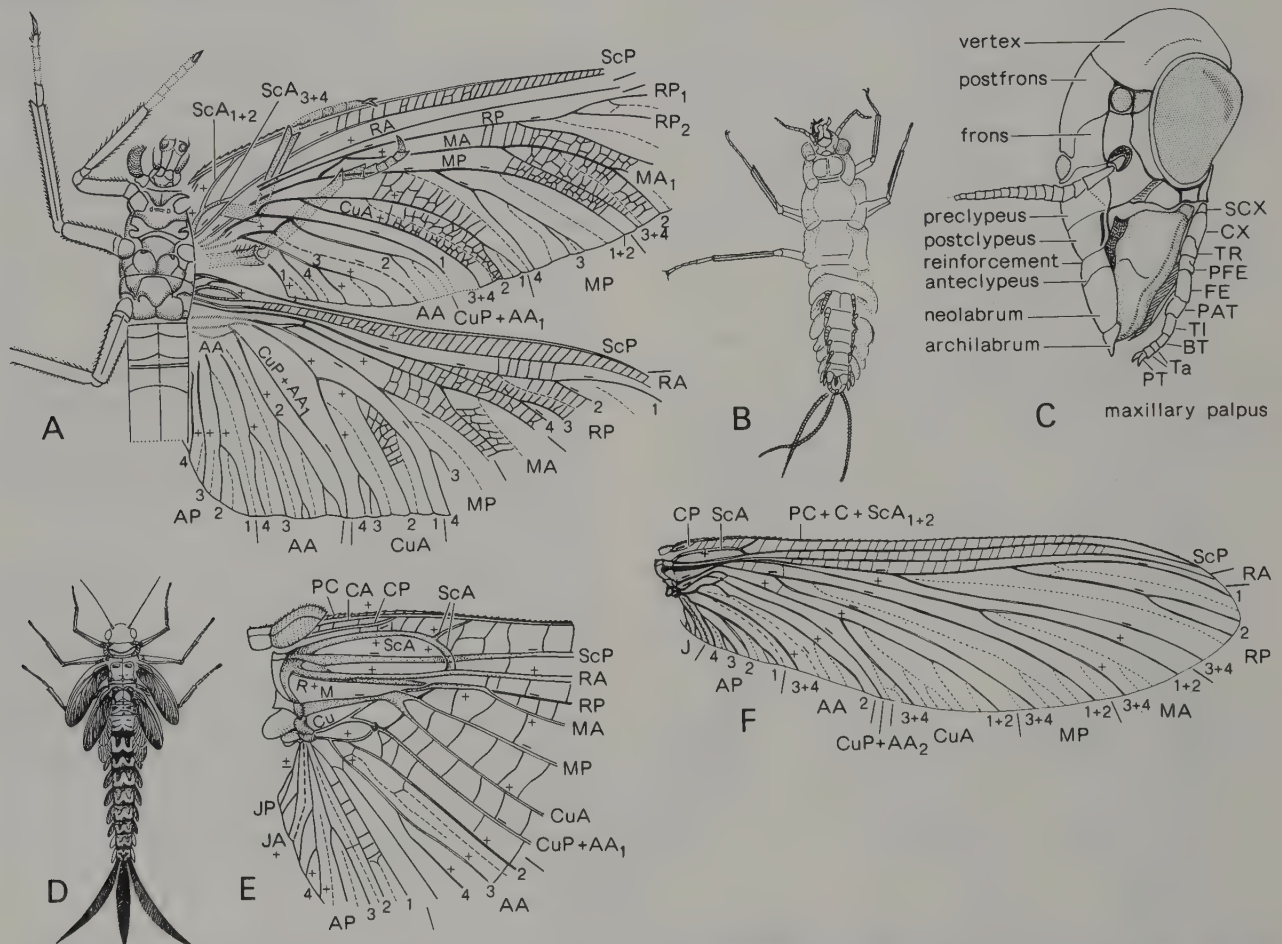


Fig. 6.14 Ephemeroptera: A, *Bojophlebia prokopi*, U. Carboniferous of Bohemia, Czechoslovakia, adult (wing span 450 mm); B, same, male nymph (body length 102 mm), with 9 pairs of both abdominal leglets and plate gills (serially homologous with wings); C, head of adult protiereismatid mayfly (composite of fossils from L. Permian of Kansas, U.S.A. and U.S.S.R.), lateral; D, *Kukalova americana*, L. Permian of Kansas, U.S.A., nymph with movable wing pads; E, *Protierisma* sp., L. Permian of Kansas, wing base with double radius (RA and RP adjacent); F, same, subadult wing. [After Kukalová-Peck 1983, 1985]

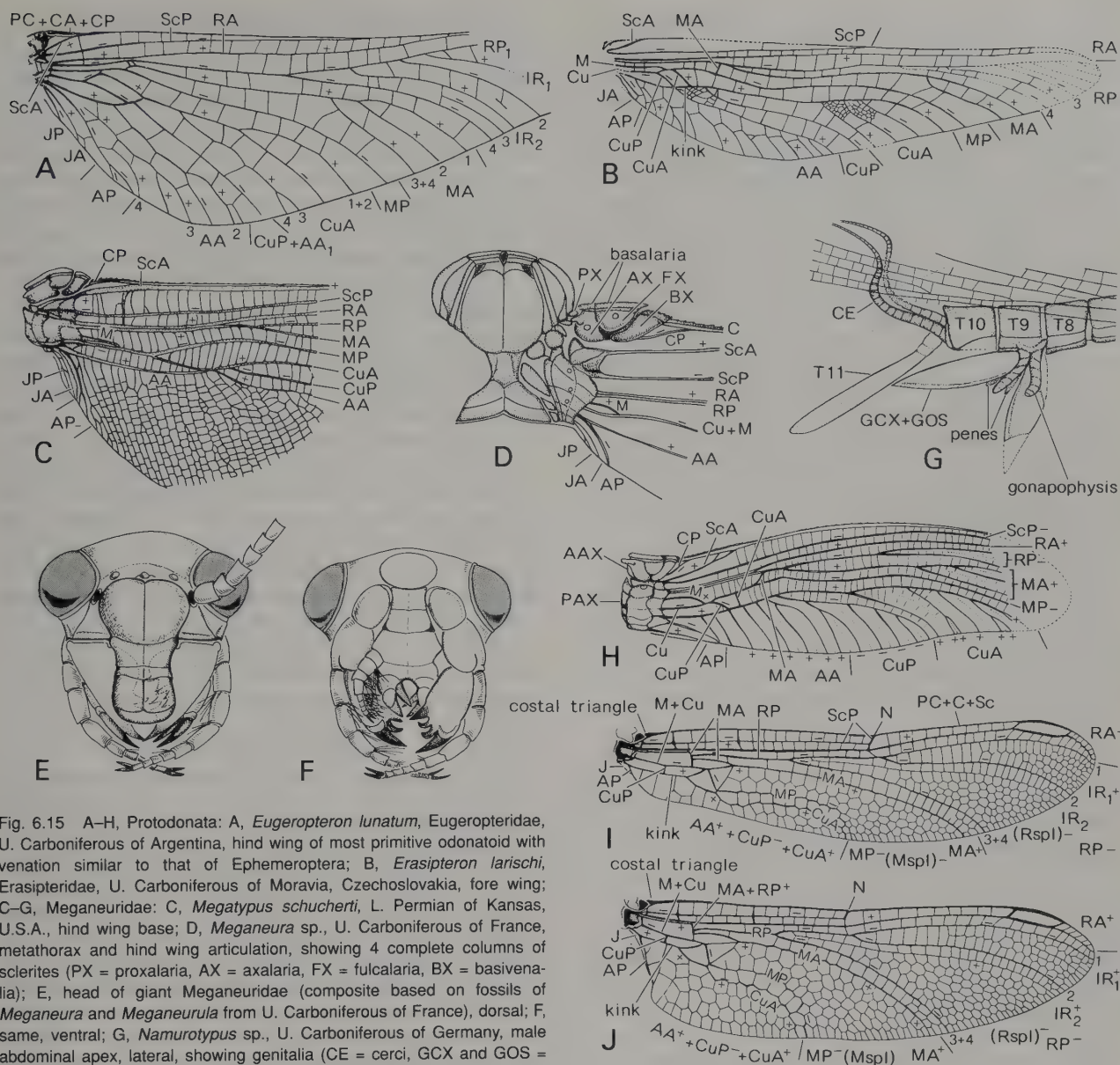


Fig. 6.15 A–H, Protodonata: A, *Eugeopterion lunatum*, Eugeopteridae, U. Carboniferous of Argentina, hind wing of most primitive odonatoid with venation similar to that of Ephemeroptera; B, *Erasipteron larischii*, Erasipteridae, U. Carboniferous of Moravia, Czechoslovakia, fore wing; C–G, Meganeuridae: C, *Megatypus schucherti*, L. Permian of Kansas, U.S.A., hind wing base; D, *Meganeura* sp., U. Carboniferous of France, metathorax and hind wing articulation, showing 4 complete columns of sclerites (PX = proxalaria, AX = axalaria, FX = fulcalaria, BX = basivenalia); E, head of giant Meganeuridae (composite based on fossils of *Meganeura* and *Meganeurula* from U. Carboniferous of France), dorsal; F, same, ventral; G, *Namurotypus* sp., U. Carboniferous of Germany, male abdominal apex, lateral, showing genitalia (CE = cerci, GCX and GOS = fused gonocoxites and gonostyli); H, articulated nymphal wing, with the anterior (AAX) and posterior (PAX) articular plates, U. Carboniferous of Illinois, U.S.A.; I, J, *Austrogomphus* sp., Recent of Australia, fore and hind wing, showing venation homologised with that of fossils and other pterygote orders (N = nodus; Mspl, Rspl = secondary veinal supplements).

[A–C, I, J after Riek and Kukalová-Peck 1984; D–F by Kukalová-Peck; G after Brauckmann and Zessin 1988 (new interpretation)]

hind legs oriented posteroventrally for grasping large prey; abdomen long, narrow; ovipositor similar to pterygote groundplan. Meganeurid males bore moderately long, annulated, S-curved cerci; a very long and probably muscled terminal appendage (T11); large, pointed, grasping lobes (gonocoxites fused with gonostyli); and short, annulated penes and gonapophyses of equal length (Fig. 6.15G) (Brauckmann and Zessin 1989). The tarsus was composed of 4 subsegments. Meganeurid nymphs (Kukalová-Peck unpubl.) had a mask (see Fig. 17.11) with prominent raptorial paraglossae and short palps, small prothoracic winglets and a remnant of the mesothoracic prescutum was retained; the mid and hind wings were fully articulated and held uplifted; older nymphs

(Fig. 6.15H) probably could fly. Abdomen with long, respiratory, segmented leglets. The venation of most primitive Eugeopteridae (Fig. 6.15A) closely resembles that of mayflies. The gigantic tropical Meganeuridae (Figs 6.15C–G) had venation enriched by secondary branches, ScA+ independent and a distinct CuP- present. About 5 Palaeozoic families occur world-wide, and about 7 occur in the Triassic of Central Asia, West Germany, France and South Africa. Protodonata include also six families assigned to the 'Protozgyoptera' (= Kennedyomorpha) and 2 to the 'Protanisoptera' (= Ditaxineuromorpha) (Pritykina 1981) from the Permian of Australia, Falkland Is, Kansas, Urals and Siberia, and U. Triassic of South Africa and Central Asia. All Protodonata have a typical

anterior axillary (= 'humeral') plate composed of distinctly separated, largely movable sclerites (Figs 6.15C, D, H), and an exposed 'double' pleural sulcus; the costal triangle, nodus and subnodus were absent (all primitive compared to Odonata) (Kukalová-Peck 1983, 1985).

Odonata (Triassic–Recent). Odonata differ from Protodonata in having: (1) completely fused sclerites in the anterior axillary (= 'humeral') plate; (2) a costal triangle incorporating ScA+; (3) the pleural sulcus covered; (4) a nodus and other kinks in the venation; (5) CuA, CuP and AA uniformly branched so that CuP is no more apparent; (6) cerci without annulation; and (7) male genitalia and cerci reduced. All of these are apomorphies. The Australian *Mesophlebia* and *Triassagrion* are among the most primitive Triassic odonate genera. Fossil Anisoptera include Liassogomphidae and Petaluridae (Jurassic of Europe, Siberia and Mongolia), Aeshnidae (Jurassic of the U.S.S.R.), Sonidae and Corduliidae (L. Cretaceous of West Mongolia) (Pritkina 1985, 1986 and others), and Mesophlebiidae (L. Cretaceous of Australia, together with Coenagrionidae (Zygoptera)). Zygoptera are recorded since the Jurassic with about 10 extinct families. Anisoptera and Anisozygoptera are possibly sister groups. The latter were richly represented in the Mesozoic of the Northern Hemisphere by about 10 families, but there are only 2 extant species. *Caraphlebia* (Anisozygoptera) is known from the Jurassic of Antarctica (Carpenter 1970).

NEOPTERA

(U. Carboniferous–Recent). Neoptera are the sister group of the Palaeoptera and in their groundplan differ from Palaeoptera in retaining the following primitive character states: M forked immediately at the base into MA and MP, venation weakly fluted with veins expressed in both dorsal and ventral wing membranes; abdominal sterna triangular (Fig. 6.3B); pregenital abdominal leglets, coxal and trochanteral abdominal endites and a coxal endite on the thoracic leg and on the cercus present in some fossil and living larvae; lacinia and galea not fused.

In the apomorphic neopterous wing articulation, sclerites from the original band are assembled into clusters (axillary sclerites, 1Ax, 2Ax, 3Ax, 4Ax; and a humeral plate; Fig. 6.16) but are still individually recognisable in Coleoptera hind wings and large Megaloptera. The proximal sclerites, however, are adjacent to or fused with the notum to form the anterior and posterior wing processes. In this derived pattern the axillary sclerites and humeral plate are not homologous with the axillary and 'humeral' plates of Palaeoptera, but they can be derived from the same groundplan (see Fig. 6.10F). In Neoptera, 3Ax, a composite of 6 groundplan sclerites, rotates and folds as the wings are pulled backwards at rest. The wings cannot be fixed for gliding without various secondary, locking devices. Another apomorphic feature of Neoptera is the permanent articulation in odonatoids (Palaeoptera) has been achieved independently. The complete detachment of a muscled sternal fragment to form the trochantin, and M closely adjacent to or fused with R (Kukalová-Peck 1983, 1985, 1987) are also apomorphies of Neoptera. Pregenital, abdominal leglets and/or some coxal and/or trochanteral endites are retained in some fossil Neoptera, some modern endopterygote embryos (Megaloptera, Mecoptera) and in polypod 'oligopod' larvae. Metamorphosis was lacking in some Palaeozoic Neoptera (mainly plecopteroids and hemipteroids).

Plecopteroid Assemblage

(U. Carboniferous–Recent). The plecopteroid assemblage contains the extinct **Protoperlaria** and **Paraplecoptera** (which probably should be subdivided into several orders) and the **Plecoptera**; the assemblage is believed to be related to Grylloblattodea (Rasnitsyn 1976, 1982; Rohdendorf and Rasnitsyn 1980) or to be the sister group of all other Neoptera (Zwick, in Hennig 1981). In the plecopteroid fore and hind wing groundplan MA and MP are stemmed (i.e. fused basally into a medial stem) and the anal area of the hind wing is expanded

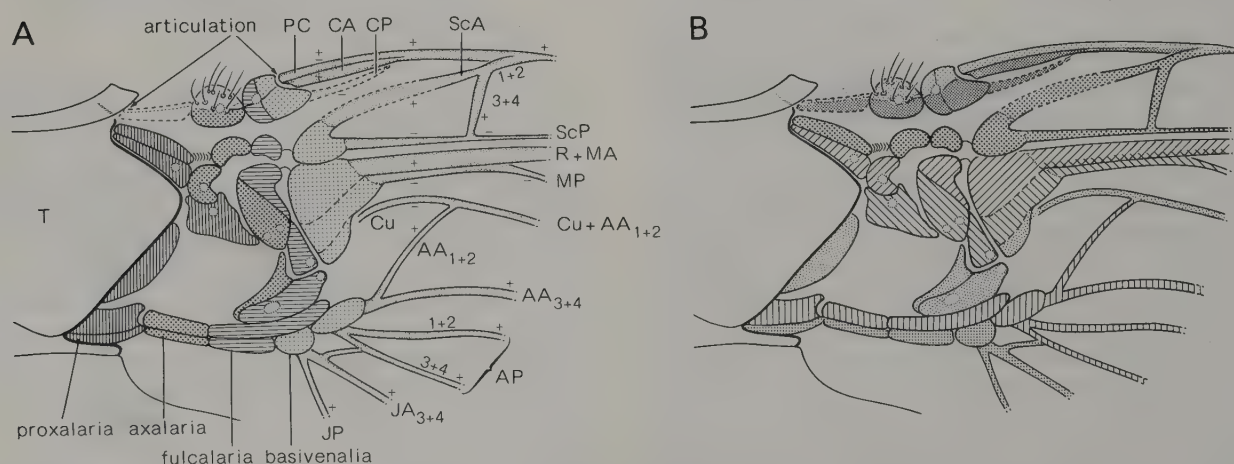


Fig. 6.16 Neopterous wing articulation groundplan based on a large, living *Corydalus* (Megaloptera) and showing the homologisation of neopterous and palaeopterous wing articulations: A, different types of shading indicating 4 columns of articular sclerites, variously fused into plates and clusters of sclerites in both Palaeoptera and Neoptera (see Fig. 1.17). B, different types of shading indicating 8 rows of sclerites aligned with the wing veins. Attachments of leg muscles (indicated by circles) compiled from diverse Recent Neoptera. [J. Kukalová-Peck]

(apomorphies). Stem-group plecopteroids (Carboniferous–Jurassic, abundant in Permian) had biting mouth-parts; prothoracic winglets well delimited from the tergum (fused to pronotum forming shield in some); and spike-like, moderately long cerci, all of which are primitive pterygote features. In the fore wings CP- and ScA+ were oblique (primitive); M had a single basal stem (apomorphic), not fused with R; MA was convex (primitive) and diverging from a concave MP (as in orthopteroids); CuA was deeply forked (primitive); there was often no brace between M and Cu (a primitive feature proving that 'M₅' is only a cross-vein); CuP was simple (apomorphic; CuP is forked in Palaeoptera and orthopteroids); AA₁₊₂ possibly was fully fused with CuP (apomorphic). The hind wing had a broadened anal lobe with AA and AP branches and a cross-vein strut between M and CuA, both apomorphic features. An implication of the wing venation observed in these fossils is that in Recent Plecoptera MA and MP are fused basally into a medial stem, but otherwise independent, and the brace between M and CuA is a secondary cross-vein (strut) and not an 'M₅' (a hypothetical, non-homologous, extra branch of M) as is sometimes suggested. Ideliidae occur in the Palaeozoic of the U.S.S.R. and the M. Triassic of Australia (*Austroidelia*); Archiprobnisidae and Megakhosaridae in the Permian of the U.S.S.R.; and Spanioderidae and Narkemidae in the Palaeozoic of the Northern Hemisphere. The Liomopteridea (Fig. 6.17A), with some 11 families, are abundant in the Permian, especially of Kansas and Europe (Carpenter 1935; Kukalová 1964). Young nymphs (Fig. 6.17B) were aquatic, with articulated wings and 9 pairs of abdominal gills, probably serially homologous with wings. Several gradual developmental series without a metamorphic instar have been documented (e.g. in *Atactophlebia*; Sharov 1957) suggesting that older nymphs were terrestrial with articulated wings and probably could fly. Palaeozoic and Mesozoic plecopteroids from the Urals and Kuznetsk Basin may or may not belong to Recent families of Plecoptera. Other fossil Plecoptera include the Euxenoperlidae from U. Permian and Triassic of S. Africa; *Stenoperlidium* from the Australian Triassic; Perlipseidae, Tshkardoperlidae and Palaeonemouridae from the Permian of Tshkarda; the Mesozoic families Siberioperlidae, Perlariopseidae and Baleyopterygidae from Asia and elsewhere (Sinichenkova 1982, 1983, 1985, 1986, 1987); and Griptopterygidae from the L. Cretaceous of Vic. (Jell and Duncan 1986). A phylogeny was offered by Sinichenkova (1987). Although modern families are known to have existed in the Eocene and the southern Notonemouridae are probably much older, the family placement of most Mesozoic fossils is uncertain (Zwick, in Hennig 1981).

Orthopteroid Assemblage

(U. Carboniferous–Recent). Orthopteroids have M stemmed in the fore wing (as in plecopteroids), then forked into MA+ and MP-, and in the hind wings MA fused near the base with R and an anal lobe with AA and AP branches (all apomorphies). In primitive orthop-

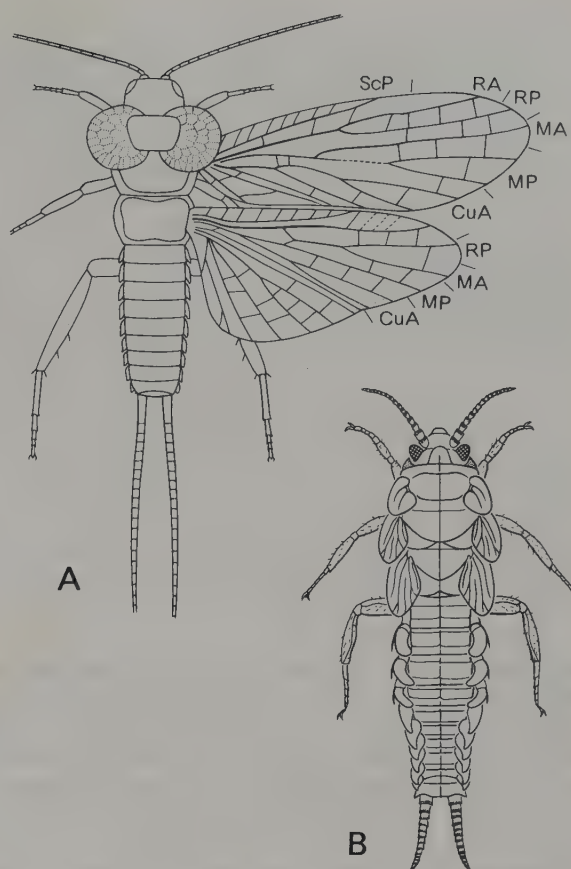


Fig. 6.17 Plecopteroid Assemblage, Liomopteridea: A, *Lemmatophora typica*, L. Permian of Kansas, U.S.A.; B, primitive aquatic nymph with articulated wings and 9 pairs of abdominal winglets serving as gills.

[A after Carpenter 1935; B after Kukalová-Peck 1978]

teroids, the wings were folded in a roof-like manner (primitive). Many Palaeozoic Neoptera have been referred to the order 'Protorthoptera'. However, this artificial group, which includes mostly insects unrelated to each other or to true Orthoptera, is gradually being dissolved, as its former constituents are assigned to surviving lineages.

Orthoptera, Phasmatodea and Embioptera share an ovipositor with the 3rd valve (gonoplac) formed by gonostyli 9 (synapomorphy). The groundplan venation, still expressed in some Recent forms, is exceedingly primitive in preserving several proto-wing features: the veinal pairs (anterior and posterior sectors) of Sc, Cu and A basally diverging without a common stem in both fore and hind wings [e.g. in Recent Acrididae (*Gastrimargus*, *Hippiscus*, *Caloptenopsis*, *Hoplolopha*) and Pyrgomorphidae (*Phymateus*)]. Orthoptera have a narrow precostal strip adjacent to C as many other primitive Pterygota, but have never had a broad 'precostal area' (Kukalová-Peck 1983). The vein usually regarded in orthopteroids as C (e.g. in Fig. 24.1) always originates from the subcostal basivenale shared with ScP- and is here homologised with ScA+ (Figs 6.18A–C). In orthopteroids the true C is weak near the base but has its own blood sinus sclerite (costal basivenale), as it does in other pterygotes. In modern

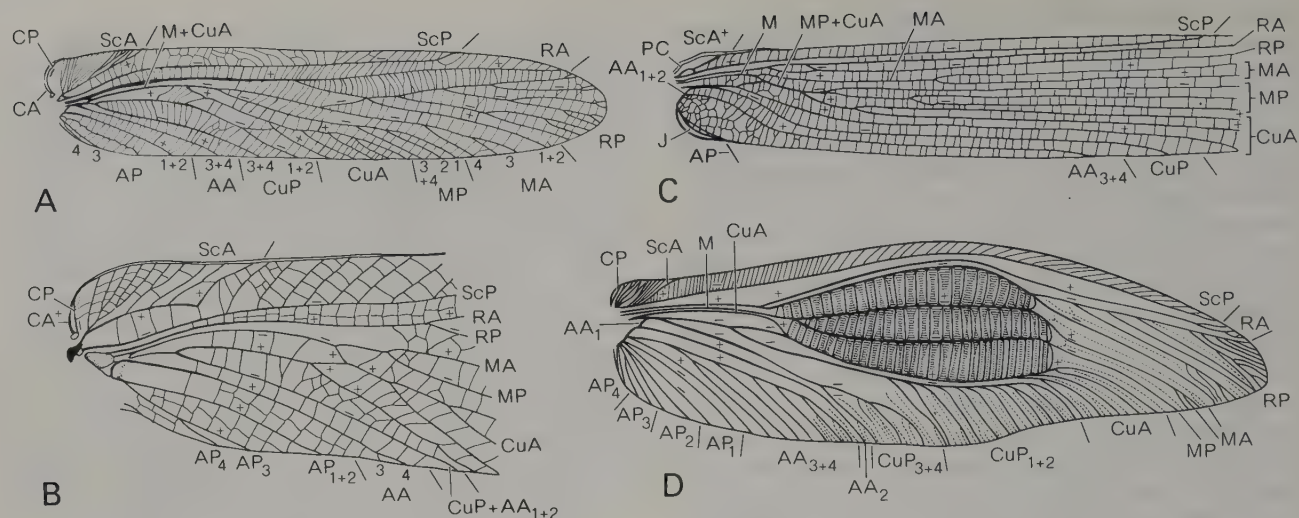


Fig. 6.18 A, B, Orthopteroid stem group: A, *Oedischia williamsoni*, U. Carboniferous of France, fore wing (composite reconstruction of wing base); B, '*Metoedischia*' sp., L. Permian of Moravia, fore wing showing different venational type; C, *Aeroplana mirabilis*, Phasmatodea, M. Triassic of Australia, fore wing; D, *Clatrotitan scullyi*, Titanoptera, M. Triassic of Australia, fore wing. [J. Kukalová-Peck]

orthopteroids, ScA has become a prominent vein to strengthen the flanks of the folded tegmina, but in many fossils ScA+ is not unusual (Figs 6.3C, 12A, 14E, F, 15H, 18A, 19C, 23A). Wings in this group often have braces (cross-veins or temporary fusions), such as that between M and CuA, and there may be a temporary fusion between RP and MA.

Orthoptera (Carboniferous–Recent). There are two types of wing venation within the early stem-group assemblage (Oedischioidea), suggesting that this group is not monophyletic and preshadowing deep differences in the seemingly uniform 'orthopteroid' venation. In the *Oedischia* type (Fig. 6.18A), Cu has no stem, CuA+ is adjacent at length basally to M, and CuP- is deeply forked. The brace is a secondary strut (+; st) between CuP₁₊₂ and CuA+. In the *Metoedischia* type (Fig. 6.18B), Cu is stemmed, CuA+ is independent from M and CuP is simple (derived). The brace is a secondary strut (+; st) between CuA+ and the stem of M-. In the hind wing groundplan the following primitive pterygote features persist: M, CuA and CuP deeply forked and independent; AA₁ is adjacent to but not fused with CuP; and AA₂ is an independent branch (the last two in calliptamine Acrididae and some other Recent forms). AA and AP in anal fan have a divided anal basivenale. Oedischioidea (Carboniferous–Triassic; Figs 6.18A, B) had jumping legs, a rather short ScA+ with serial branches, and an arched, basally strong C. Stridulatory organs were present in L. Permian species. Early Ensifera occur in the Permian of North America (Permoraphidiidae) and the Triassic of Australia and the U.S.S.R. (Triassomanteidae). Elcanidae, which are related to Permoraphidiidae, are often found in the Permian, Jurassic and Cretaceous of the Northern Hemisphere (Zessin 1987). About 12 other families are known only from the Mesozoic. Tettigonioidae are found in the U. Permian of the Ural Mts and South Africa (Tettavidae and Kamiidae), and the Mesozoic of Eurasia (Vitimiidae and Bintoniellidae). The oldest Grylloidea

occur in the U. Triassic of Kirgizia, together with an extremely varied fauna of other orthopteroids (Sharov 1968, 1971). *Prohagla*, *Neohagla* (Haglididae), Gryllacrididae and Xenopteridae occurred in the M. Triassic of Australia, and Proparagryllacrididae in the Triassic of Australia, the U.S.S.R. and South Africa. Haglids are abundant in the Mesozoic. Locustopseidae have been found in the U. Permian of South Africa, L. Triassic of Siberia and Central Asia, M. Triassic of Australia, and Jurassic of Europe and Asia (Zessin 1983; Zherikhin 1985). A gryllacridoid and tridactylid are known from the L. Cretaceous of Vic. (Jell and Duncan 1986). Tridactyl-oidea also occur in the L. Cretaceous of the U.S.S.R. Fossil Acridoidea are known only from the Tertiary. A phylogeny of Orthoptera was proposed by Gorokhov (in Ponomarenko 1988).

Phasmatodea (Triassic–Recent). Stick insects are strongly autapomorphic orthopteroids which originally had long, narrow fore wings and slightly broadened hind wings (Sharov 1968, 1971). In the groundplan, veins are arranged in parallel and short branches near the posterior margin are eliminated. Primitive orthopteroid features retained in the fore wing are the moderately long ScA, originally with branches, the stemmed M, and MA+ being independent of RP. Derived features are the probably short-stemmed Cu, CuA braced with MP by a temporary fusion, and CuP fused with AA₁₊₂. AA₃₊₄ is simple and AP is branched. The hind wing venation is similar, but CuP is fused with AA₁, while AA₂ remains independent (very primitive), and AA₃₊₄ and AP are branched to fill up the progressively enlarged anal fan (autapomorphy of Phasmatodea). Xiphopteridae, Chresmodidae and Aeroplanidae are diverse in the U. Triassic of Kirgizia. *Aeroplana* (Aeroplanidae) occurred in the M. Triassic of Australia (Fig. 6.18C). Aerophasmatidae are known from the U. Jurassic of Karatau and England, while Cretophasmatidae occur in the U. Cretaceous of Karatau and Greenland (Birket-Smith 1981). Phylliidae have been

found in Baltic amber and in the Miocene of Europe and the U.S.A. Phasmatodea may have been derived before the Permian from an ancestor more primitive than the Oedischiidea.

Titanoptera (Triassic). Gigantic orthopteroids with wingspan up to 36 cm; fore legs raptorial; mandibles long, sharp; and wings folded flat over the abdomen (all apomorphies within the orthopteroid assemblage). Males had prominent, fluted, mirror-like, resonating areas in fore wings (also derived). Groundplan venation: ScA+ moderately long; M stemmed, adjacent to R; Cu not stemmed (primitive); CuA basally adjacent to M, diverging before M divides, then CuA running close to CuP₁₊₂ and connected to it by a strut (an apomorphy); CuP deeply forked as in some oedischiids and both concave branches further branched (a very primitive feature); AA₁ fused with CuP; AA₂ independent, simple (primitive); AA₃₊₄ and AP richly branched (primitive); resonating area between RP and CuA, with MA and MP either crossing it or close together and shifted anteriorly. Hind wing with similar venation but without a resonating area and with anal fan filled with branches of AA₃₊₄ and AP. Titanopteran venation cannot be derived from any other known orthopteroids. Paratitanidae, Gigatitanidae and Clatotitanidae occur in the U. Triassic of Kirgizia (Sharov 1968, 1971). The last-mentioned family is represented in the M. Triassic of Australia by the spectacular *Clatotitan* (Fig. 6.18D).

Embioptera (L. Permian–Recent). Venation reduced compared to the orthopteroid groundplan. Embiopteran

groundplan venation (Fig. 6.19A) has a strong, typically orthopteroid ScA+; ScP closely follows RA; M is stemmed; MA is adjacent basally to RP; and CuA approaches the stem of M near its base. Apomorphies of Embioptera include the absence of all veins except AP₁₊₂ from the anal area of the fore wing and the loss of the anal fan from the hind wing. Undescribed embiids with typical asymmetrical male genitalia are known from the L. Permian of the Urals, U.S.S.R. (Fig. 6.19B). Tertiary occurrences are mostly in amber, and all except the Eocene *Burmitembia* from Burma and the Oligocene *Litembia* from the U.S.A. (Ross 1984) are similar to modern forms.

Zoraptera (U. Eocene?–Recent). The phylogenetic position of this order, which contains the single genus *Zorotypus*, is uncertain (see previous chapter). A fossil zorapteran has been described from Dominican amber, which has been dated as either U. Eocene or L. Miocene (Poinar 1988).

Blattoid Assemblage

(U. Carboniferous–Recent). Blattoids, hemipteroids and endopterygotes all have M forked close to the wing base (primitive) and MA fused with R over a considerable length (synapomorphy), but the extended anal lobe in the hind wing filled only with AP branches (Figs 6.19D, 20A) is a blattoid apomorphy. Other derived features of the blattoid assemblage include their ability to fold their wings more or less flat over the abdomen and their distinct, curved, fore wing claval furrow. The brace between

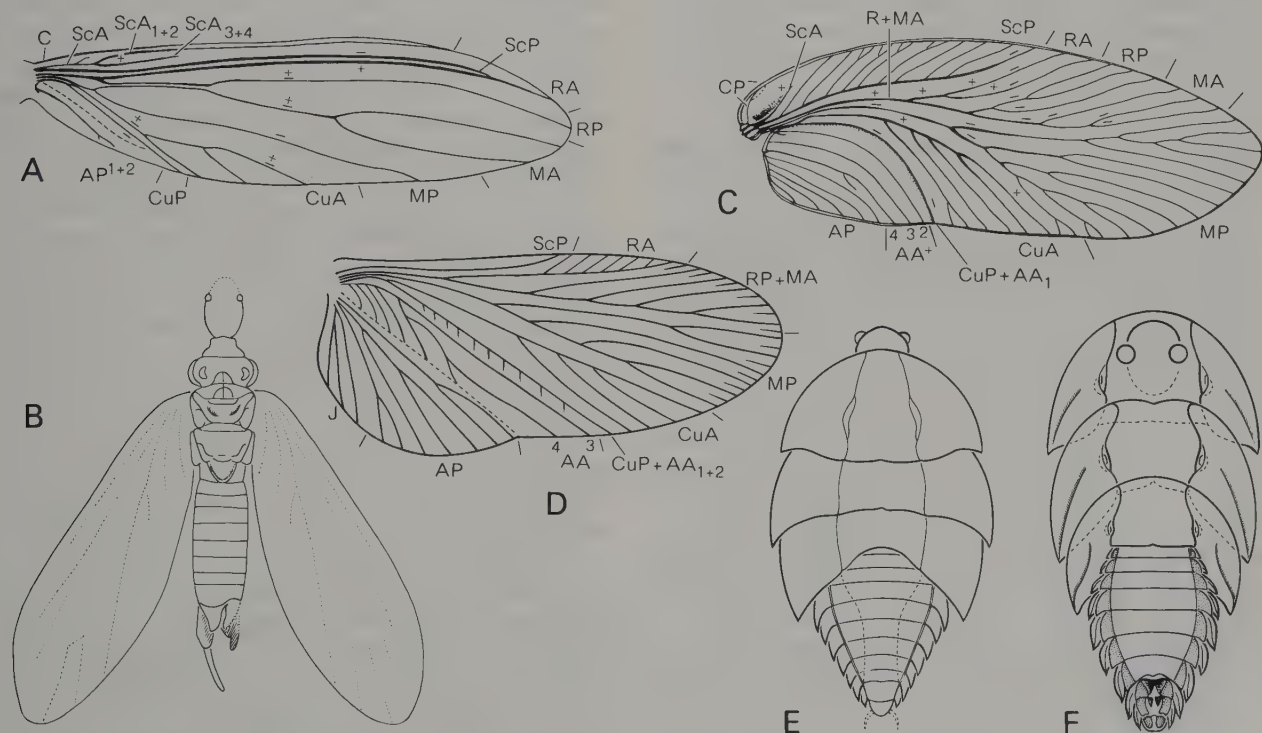


Fig. 6.19 A, B, Embioptera: A, *Clothoda longicauda*, Clothodidae, Recent, fore wing; B, undescribed male, L. Permian of Ural Mts, U.S.S.R. C–F, Blattodea stem group: C, *Phylloblatta* sp., Archimylacridae, U. Carboniferous of New Mexico, fore wing; D, *Puknoblattina* sp., L. Permian of Kansas, U.S.A. (new interpretation); E, F, primitive blattoid nymph, U. Carboniferous of Illinois, U.S.A., dorsal and ventral. [A–C, E, F by Kukalová-Peck; D after Schneider 1984]

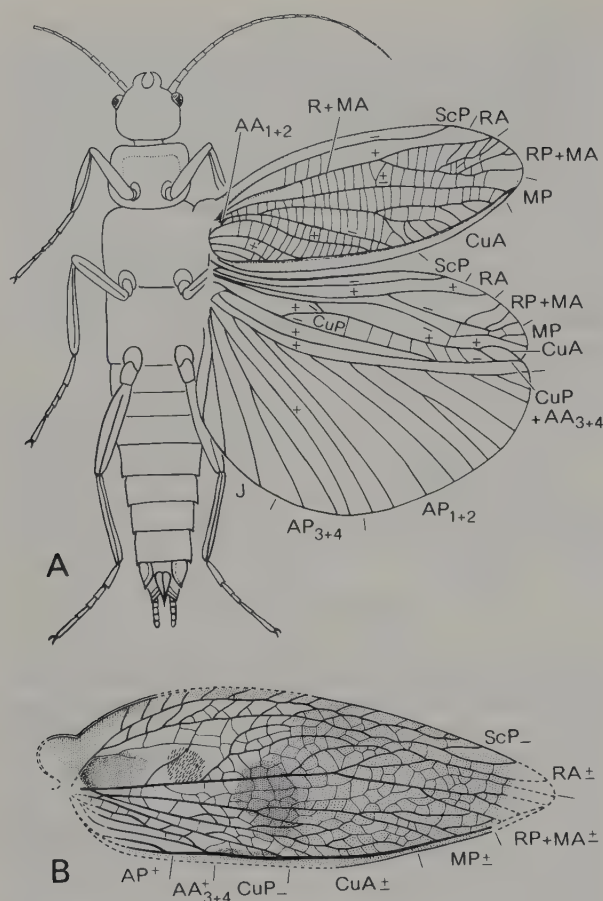


Fig. 6.20 Protelytroptera: A, *Apachelytron transversum*, L. Permian of Moravia; B, *Phyllelytron petalon*, Protocoleidae, U. Permian of Australia. [A by Kukalová-Peck; B after Kukalová 1966]

M and Cu, which has been acquired in hemipteroids and endopterygotes, is absent in blattoid fore wings. Cockroach-like tegmina of the blattoid stem group (Figs 6.19C–F) are very common among Palaeozoic fossils from tropical deposits in the Northern Hemisphere (Schneider 1984); hind wings are less common. These tegmina often bear a striking resemblance to fern leaves. The heads of these stem-group blattoids were pro-, hypo- or opisthognathous and more or less covered by the pronotum. In the tegmina ScP- was ribbon-like, the anals reached the posterior margin, and AA₂ ran free (all primitive pterygote features). The anal area in the hind wing folded in a unique way, flatly beneath the rest of the wing along the simple, straight anal fold between AA and AP (an apomorphy of the stem group), while AA₁₊₂ fused with CuP and AA₃₊₄ bore pectinate branches (Fig. 6.19D). The ovipositor was long and thin. The largest family was the Archimylacridae, including the cosmopolitan *Phyloblatta* (Fig. 6.19C) and many other genera. All nymphs were terrestrial and had wings firmly fused with the terga (a derived condition); metamorphosis must have taken place in these. However, in some nymphs sutures persisted between the wings and the terga (Figs 6.19E, F). The Palaeozoic 'order' Protoblattodea is a group of conve-

nience, into which forms similar in some features to cockroaches have been placed.

Blattodea (U. Carboniferous–Recent). In Blattodea, ScA+ forms a blunt, strong ridge, ScP is short and oblique, the anals end at CuP, and the anal area in the hind wing folds in a fan-like manner (all apomorphies). AA₃₊₄ sometimes bears a conspicuous long fork which runs parallel to the fused CuP and AA₁₊₂. The Mylacridae and Neorthroblatinidae (U. Carboniferous–Permian) had venation typical of modern Blattodea. Probable oothecae are known from the Carboniferous. The extinct Poroblattinidae are common in the Permian, and *Triassoblatta* is known from the Triassic of Australia, Tas. and South Africa. Mesoblattinidae were dominant in the Northern Hemisphere from the U. Carboniferous to the end of the Jurassic, and lived also in the U. Triassic of South Africa. Jurassic cockroaches are known from Siberia and Mongolia (Vishniakova 1985), and Chinese forms (U. Permian) have been described by Lin (1978). Most Recent families extend back to the early Caenozoic, but are probably older.

Isoptera (L. Cretaceous–Recent). Termites evolved from Palaeozoic blattoids from which they inherited distinctive venational features, still retained in *Mastotermes*: anal veins in tegmina reach the posterior margin; anal area in hind wings folds flatly under, along the anal fold; AA₃₊₄ with pectinate branches. The oldest, undisputed termites are Hodotermitidae from the L. Cretaceous of Labrador (Emerson 1968), southern England, Lebanon (Jarzembowski 1981) and France, and the U. Cretaceous of Siberia (Zherikhin and Sukacheva 1973). In the Tertiary, *Mastotermes*-like termites were distributed world-wide. Hodotermitidae are known from the L. Cretaceous of Spain and from the Oligocene of Montana, U.S.A. (S. E. L. Lewis 1973). Recent families probably originated in the Mesozoic (Emerson and Krishna 1975).

Mantodea (Eocene–Recent). Praying mantids retain several pterygote features lost in all other blattoids: anterior ocellus present; ScA+ unmodified and Cu without a stem. The conspicuous anal fold and well-developed jugal lobe in the fore wings are apomorphies of Mantodea. Mantids probably arose from L. Carboniferous blattoids, but their fossil record before the Tertiary is uncertain. Recent families occur sporadically, for instance in Eocene Baltic amber.

Protelytroptera (Permian–L. Cretaceous). This diverse stem group, containing the probable ancestors of Dermaptera, occurs in all Palaeozoic climatic zones. Their primitive tegmina had a sclerotised, expanded area around ScA+ and a typical, incised, blattoid claval furrow; their hind wings resembled closely those of Palaeozoic cockroach-like blattoids (Fig. 6.20A). They had a hypognathous head and outer ovipositor. Four families [Protocoleidae (Fig. 6.20B), Permophilidae, Labidelytridae (= Stenelytridae, see Kukalová-Peck 1988b) and Dermelytridae] lived in the cold climate of the Australian U. Permian (Carpenter and Kukalová 1965; Kukalová 1966), and the first two of these occurred also in South Africa. Protocoleid venation strongly resembles the weakly indicated venation in the tegmina of Recent

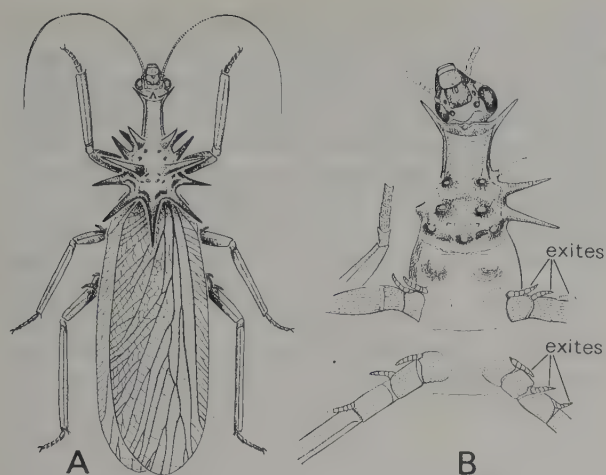


Fig. 6.21 Hemipteroid Assemblage: A, *Gerarus danielsi*, Geraridae, U. Carboniferous of Illinois, U.S.A.; B, same, head and thorax, dorsum removed. [After Kukalová-Peck 1987]

Labiduridae. The L. Cretaceous *Umenocoleus* (Umenocoleidae) from Kansu, China, was placed by its describers (Chen and T'an 1973) in the Coleoptera but has the elytral (tegmenal) venation characteristic of Protelytroptera.

Dermaptera (U. Jurassic–Recent). Primitive earwig tegmina are bent anteroventrally along R, reinforcing most of the anterior margin. The bent anterior part resembles the costal area of cockroaches. In the hind wings ScP, R, M, CuA and CuP run parallel and close to each other, while mainly AP_{1+2} , AP_{3+4} and J radiate to support the enormous anal fan. The oldest earwigs from the U. Jurassic of Kazakhstan belong to both the extinct suborder Archidermaptera (Protodiplatyidae) and the extant Forficulina [subfamily Semenoviinae of the modern family Pygidicranidae (Vishniakova 1980)]. Other forficuline fossils include *Mesoforficula*, from the Jurassic of Siberia (Vishniakova 1980, 1985) and Cretaceous of China, and *Labiduromma* from the Oligocene of Colorado (Brown 1984).

Grylloblattodea (? U. Carboniferous–Recent). Palaeozoic and Mesozoic families assigned to Paraplecoptera and Protoperlaria, including also the early Mesozoic Geinitziidae from Central Asia, Siberia and Australia, all winged, are said to be related to Grylloblattodea, the modern species of which are apterous (Rasnitsyn 1976, 1982; Rohdendorf and Rasnitsyn 1980).

Hemipteroid Assemblage

(U. Carboniferous–Recent). The most outstanding autapomorphy of the hemipteroids is the specialisation of the head and mouth-parts for piercing and sucking. They have a highly domed postclypeus, to accommodate cibarial musculature, and diverse mouth-parts; the mandibles are variable and often stylet-like. Hemipteroids adapted to dry land and their fully terrestrial nymphs lost the abdominal, leg-derived appendages. The hemipteroid assemblage probably is the sister group of Endopterygota (Hennig 1981), based on two synapomorphies: the forking of M at its very base, with MA becoming fused to R, and the presence of a brace (cross-vein or fusion) between

MP and CuA. The first feature and a deep claval fold are also shared with the blattoids. Hemipteroids and Endopterygota show many similar trends: invagination of the meso- and metathoracic sterna to form a cryptosternum; diminution or loss of the cerci; looping of veins in the anal area; expansion of the precostal strip of the wing forming an epipleuron (in Auchenorrhyncha and Coleoptera); development of quiescent and/or non-feeding metamorphic instars (Endopterygota, Thysanoptera, Aleyrodidae and Coccoidea); wings tending to develop as subcuticular anlagen (Thysanoptera, some Auchenorrhyncha, Endopterygota); occasional presence of macrotrichia. Significantly, in the groundplan of both hemipteroids and Endopterygota (and unlike other Pterygota), the hind wings are similar to the fore wings, lack a vanus, and fold solely along the jugal fold into a roof-like position (but coleopterous hind wings fold along the anal fold). Post-Palaeozoic, hemipteroid hind wings fold through the anal system. In the fore wing, PC is adjacent to C, as a precostal strip, and CP- and ScA+ are rather short and oblique (all primitive features), but CP- may become quite prominent and ScA disappear in the tegminous fore wings of early Hemiptera. In primitive hemipteroids, MP follows closely R, diverges and braces with CuA, usually by means of a short strut (arculus) or by direct temporary fusion (derived); the base of CuA (in Cicadomorpha: Ignotalidae) or the base of MP (in modern Cercopoidea) is sometimes reduced.

The Palaeozoic hemipteroid assemblage contained many strongly autapomorphic side-branches, often with a highly domed postclypeus; short, annulated cerci; and a primitive, striated cutting ovipositor. Mouth-parts were diverse, sometimes with specialised, chisel-like laciniae supporting the mandibles (Fig. 6.22c). The tegmina were folded roofwise (primitive in pterygotes) or overlapping. MP_{3+4} was often fused at length with CuA (derived), or CuP was forked and CuP_{1+2} braced with CuA; a clavus

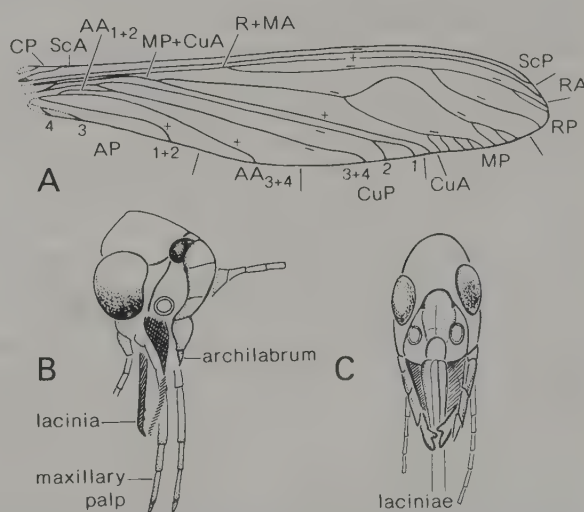


Fig. 6.22 Hemipteroid Assemblage: A, *Aspidoneura flexa*, Caloneuroidea, L. Permian of Kansas, U.S.A., fore wing; B, *Paleuthygramma tenuis*, Caloneuroidea, L. Permian of Urals Mts, U.S.S.R., head, lateral, showing long lacinia; C, *Synomaloptila longipes*, Synomaloptilidae, L. Permian of Ural Mts, head, frontal, showing chisel-like laciniae. [J. Kukalová-Peck]

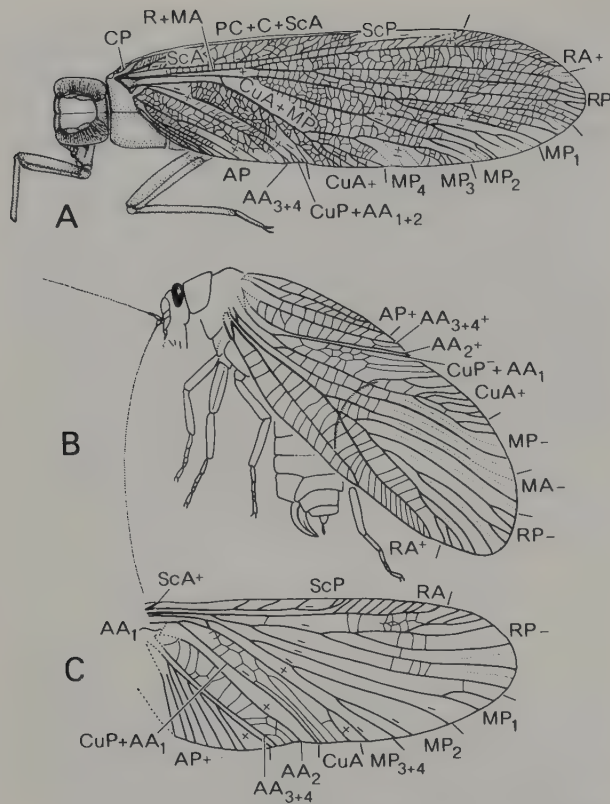


Fig. 6.23 Hemipteroid Assemblage: A, *Protoblattina bouvieri*, Paoliidae, U. Carboniferous of France, dorsal; B, *Glaphyrophlebia uralensis*, Blattinopsodea, L. Permian of Ural Mts, U.S.S.R., lateral; C, *G. subcostalis*, L. Permian of eastern Europe, hind wing.

[A after Kukalová-Peck 1983; B, C after Rasnitsyn 1980 (new interpretation)]

(= pointed anal area) was more or less pronounced and anal loops were often present; CuP was fused only shortly with AA in primitive forms; later it became adjacent to AA₁ while AA₂ remained free, and finally, CuP and AA₁₊₂ became fully fused. Geraridae (Figs 6.21A, B) had a domed postclypeus, heavy protective spines, thoracic exites, a narrow abdomen, a striated ovipositor and short cerci; while Cacurgidae had prolonged, triangular mouthparts (Brauckmann *et al.* 1985). Herdiniidae (Fig. 6.6) had very primitive nymphs with fully articulated wings which probably were capable of flight. Paoliidae (Fig. 6.23A) held their wings roof-like in the Namurian (early U. Carboniferous), but the wings overlapped in Westphalian (mid U. Carboniferous) forms. Synomaloptilidae (Fig. 6.22C) had chisel-like laciniae as in Psocoptera, triangular mandibles and veins covered with setae as in Fulgoroidea and Endopterygota. Caloneuroidea (Figs 6.22A, B) had long, serrated laciniae and a long prefemur/femur. Blattinopsodea (Figs 6.23B, C) had a nodal line and striated ovipositor. Glosselytroidea, including Permoberothidae from U. Permian of Australia, had the costal area more or less broadened near the base as in Peloriidae (Fig. 6.25J), a narrow clavus with occasional anal loops, and veins covered with setae.

Psocoptera (Permian–Recent). This order is close to the hemipteroid stem group but has derived (simplified)

wing venation. The Palaeozoic Permopsocina (Fig. 6.24A) had a short, tapering, sucking rostrum with triangular mandibles (derived), but had primitive, subequal wings, a pterostigma sometimes not sclerotised, an arculus present and MP forked twice. Permopsocina survived until the L. Cretaceous, when they were represented by the Archipsyllidae (Vishniakova 1976). Recent suborders of Psocoptera probably originated in the Jurassic. Psocina were found in the U. Jurassic of Karatau; Trogiidae, Amphientomidae, Lachesillidae and other families are represented in Cretaceous amber from Lebanon and India. U. Cretaceous resin from Siberia has yielded Amphientomidae, Trogiidae, Psyllipsocidae,

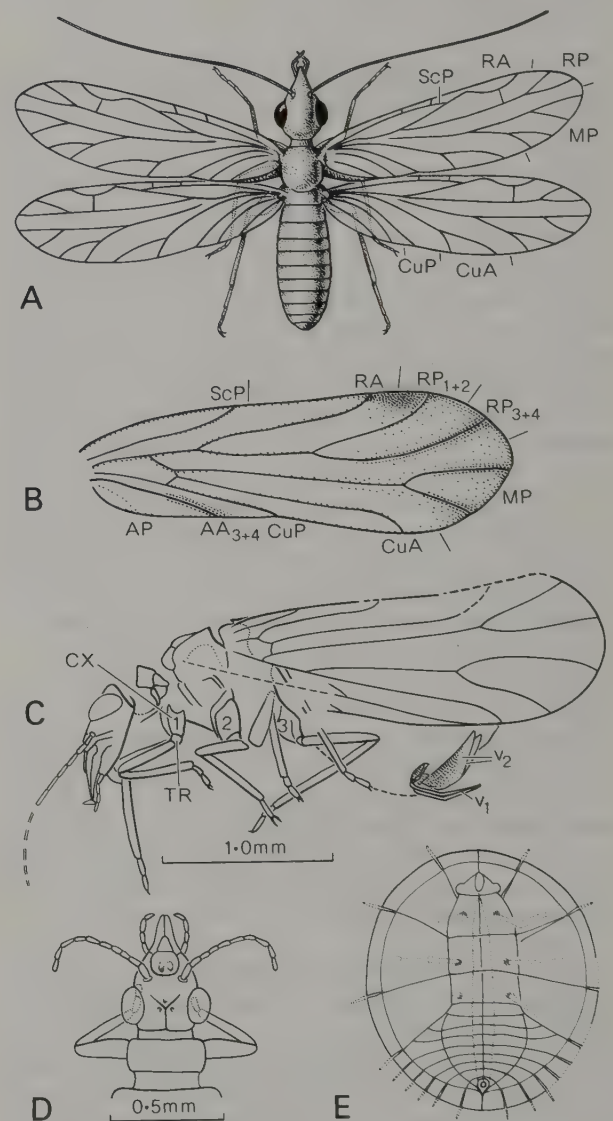


Fig. 6.24 A, Psocoptera stem group, Permopsocina: *Dichentomum tinctum*, L. Permian of Kansas, U.S.A.; B–D, Thysanoptera stem group, Lophioneurina: B, *Zoropsocus pilosus*, U. Permian of Kuznetsk Basin, U.S.S.R., fore wing; C, *Z. itschetuensis*, Jurassic of Kazakhstan, U.S.S.R., lateral (V1, V2 = ovipositor); D, same, head and thorax, dorsal; E, ? Aleyrodina: the oldest, cone-shaped, sternorrhynch nymph, L. Permian of South Africa.

[A after Carpenter 1933; B–D after Vishniakova 1981; E by Kukalová-Peck]

Thysanoptera (Permian–Recent). Thrips embryos are equally similar to Psocoptera and Hemiptera, with many unique features (Haga 1985). Members of the Lophioneurina [e.g. *Zoropsocus* (Figs 6.24B–D), *Cyphoneura*, *Lophioneura*; Permian–Cretaceous] had symmetrical, conical mouth-parts (Vishniakova 1976, 1981). The U.

Hemiptera (Permian–Recent). Mouth-parts bristle-like

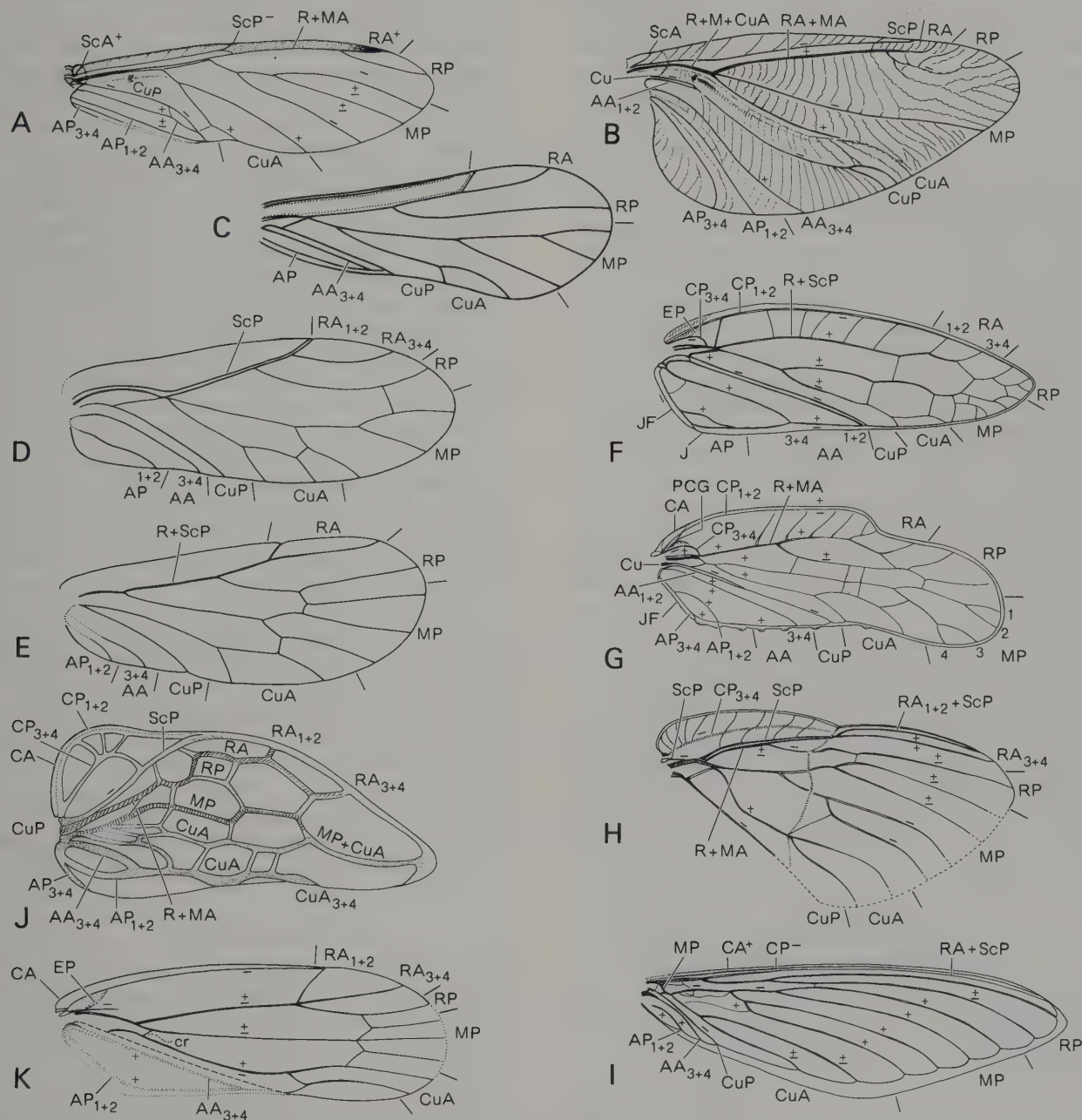


Fig. 6.25 A, Aphidina stem group: *Triassoaphis cubitus*, M. Triassic of Australia, wing. B, Coccina: venational scheme of a Recent Margarodidae. C, Protopsyllididae. *Tomiopsyllidium iljinskienae*, U. Permian of Kuznetsk Basin, U.S.S.R., wing. D, E, Hemiptera stem group, Archescytinidae: D, *Pernopsylla grandis*, L. Permian of Kansas, U.S.A., fore wing; U, *Archescytina permiana*, L. Permian of Kansas, U.S.A., hind wing. F-I, Auchenorrhyncha fore wings, M. Triassic of Australia: F, *Ipsivia jonesi*, Scytinopteroidea, Ipsicidae (EP = epipleuron, shaded); G, *Dysmorphoptiloides elongata*, Prosboloidea (JF = jugal fold, PCG = groove involving PC in epipleuron); H, *Fletcheriana triassica*, Palaeoptinoidea, with a groove after CP3+4; I, *Mesogereon superbum*, Cicadomorpha stem group. U, *Howeria kingsmilli*, Peloridiidae, Recent, Lord Howe I., fore wing; K, Heteropteroidea stem group: *Actinoscyntia belmontensis*, Progonocimicidae. U. Permian of Australia, fore wing.

[A-C, F-K by Kukalová-Peck; D, E redrawn after Carpenter 1933, 1939]

and derived from elongate stylet-like mouth-parts similar to those of early psocopterans. The Permian Archescytinidae (Figs 6.25D, E) are believed to belong to the stem group. They retain similar fore- and hind wings but have somewhat impoverished, derived venation. The phylogeny of homopterous Hemiptera was discussed by J. W. Evans (1963a) and Shcherbakov (1984, 1985).

STERNORRHYNCHA (Permian–Recent). Fossil Aphidoidea can be recognised by their narrow wing base. The oldest undisputed aphid wing is *Triassoaphis* (Fig. 6.25A) from the M. Triassic of Australia (J. W. Evans 1971a). Genaphididae occur in the U. Jurassic of England and Karatau (Shaposhnikov 1979). Recent Drepanosiphinae are known from Karatau. Jurassic aphids were found in southern Siberia and western Mongolia (Shcherbakov 1985). By the U. Cretaceous, Aphidoidea had radiated. Oviparosiphidae are known from the L. Cretaceous of Mongolia (Shaposhnikov 1985). The U. Cretaceous of Taimyr (U.S.S.R.) has yielded 5 extinct families, as well as the extant Drepanosiphinae, Pemphiginae and Aphididae (Kononova 1975, 1976, 1977). Palaeoaphididae and Drepanosiphinae occur in the U. Cretaceous of Canada (W. R. Richards 1966). Elektraphidiidae from Baltic amber are related to Phylloxeridae. Coccoidea (Triassic–Recent) are the sister group of Aphidoidea with wing venation similar to primitive aphids (Fig. 6.25B). *Mesococcus* from the L. Jurassic of Issyk-Kul, is doubtfully a coccoid. Male coccoids have been found in the L. Cretaceous of Baissa, U.S.S.R. (Koteja unpubl.), and *Electrococcus* (Margarodidae ?) occurs in the U. Cretaceous of Canada (Beardsley 1969). Tertiary scale insects belong to modern families. Psylloidea possibly date from the Permian. Protopsyllidiidae (Fig. 6.25C) are known from the U. Permian of the U.S.S.R. and Australia, M. Triassic of Australia, L. to U. Jurassic of Asia, U. Jurassic of England (*Aphidulum*) and L. Cretaceous of Mongolia. They have a blade-like ovipositor and relatively rich venation and may belong to the stem group of Sternorrhyncha. *Liadopsylla* from the Jurassic of Germany and Karatau and the L. Cretaceous of Mongolia (Shcherbakov 1988a) has the derived genitalia and the head capsule of Psylloidea. The phylogeny of fossil psyllids is discussed by Szelegiewicz (1971) and Bekker-Migdisova (1985). The Aleyrodoidea (U. Permian–Recent) are the sister group of the Psylloidea. Possibly the oldest whiteflies (Fig. 6.24E; still undescribed) are known from the U. Permian of South Africa. The doubtful *Aleuonympha* was described from the U. Permian of South Africa, and *Permaleurodes* from the U.S.S.R. Ancestors of Recent forms were recorded in the L. Cretaceous of Lebanon (Schlee 1970).

AUCHENORRHYNCHA (Permian–Recent). Auchenorrhyncha and Coleorrhyncha + Heteroptera are close embryologically (Haga 1985) and share three derived traits: (1) in the hind wing, a vannus (= broadened anal area) (Wootton and Betts 1986); and in the tegminous fore wings: (2) a long, strong CP₁₊₂ running in parallel to CA and (3) ScA+ completely absent (Figs 6.25F, G). The mouth-parts are highly derived: the mandibles have lost their posterior articulation; the mandibles and laciniae are

bristle-like; and the galeae and hypopharynx serve as clamps (E. L. Smith, in Kukalová-Peck 1983). In the groundplan, Auchenorrhyncha retained the ancient pre-costal strip (PC), which sometimes widens anteroventrally into an 'epipleuron'; as PC thickened and shifted posteroventrally, a veinless groove sometimes formed in the dorsal membrane posterior to CP (Fig. 6.25). In many fossils, CP- is prominent. CP- forks with CP₁₊₂ parallel to C and CP₃₊₄ running from the costal basivenale to ScP in a short arch (Fig. 6.25F). In Fulgoroidea (and weakly indicated in fossil Cicadoidea, Fig. 6.25H), CP- may look like a false 'subcosta' with serial branches. ScP- supports R (an apomorphy of Auchenorrhyncha; in Heteropteroidea ScP- is independent of R). The brace between MP and CuA (arculus) is a strut (cross-vein). Secondly, MP may fuse with CuA (derived). Jumping legs also may have been part of the auchenorrhynchan groundplan. The oldest fossil Auchenorrhyncha are from the L. Permian of Moravia (Czechoslovakia), the Ural Mts and Kansas, and the U. Permian of the Kuznetsk Basin. A phylogeny of the Cicadomorpha was proposed by Shcherbakov (1984). Scytinopteroidea (Fig. 6.25F) and Prosboloidea (Fig. 6.25G) are the largest groups of Palaeozoic cicadomorphs. Twelve or more families occur in U. Permian, almost all in the temperate climate of Angara and Gondwana, especially at Belmont, Australia (mainly Prosbolidae) but also in South Africa. One specimen is known from Antarctica (Tasch and Riek 1969). Early cicadomorphs, e.g. Hylicellidae and Chilocyclidae, occurred from the Triassic to the Cretaceous in Australia and Central Asia (Shcherbakov unpubl.). Highly specialised, weakly flying or wing-shedding Mesogereonidae (Fig. 6.25I) have been found in the Australian and South African Triassic; Ipsviciidae (Fig. 6.25F) occur in the Triassic and also in the L. Jurassic of Issyk-Kul. The earliest Cicadoidea is *Liassocicada* from the U. Triassic of England (Whalley 1983) and the first certain tettigarctid, *Cicadoprobole*, occurred in the L. Jurassic of Issyk-Kul. The gigantic Triassic *Fletcheriana* from Australia and South Africa (Fig. 6.25H) belongs to the Dunstaniidae (Palaeontinoidea) (Shcherbakov 1984). The L. Triassic of Siberia has yielded Cixiidae, and the U. Triassic, Cixiidae, Ricaniidae and many Cicadomorpha. Numerous Jurassic Auchenorrhyncha from Asia were described by Shcherbakov (1985). *Eotettigarcta* (Tettigarctidae) is from the U. Cretaceous of Scotland. The first Cercopoidea are the Procercopidae from the L. Jurassic of Germany and Issyk-Kul. The earliest leafhoppers (Cicadelloidea) are known from the M. Jurassic of Siberia. Cicadellidae (*Myangadina*) occur in the L. Cretaceous of Mongolia (Shcherbakov 1986). Jascopidae, which may be intermediate between Cercopidae and Cicadellidae, occur in the U. Cretaceous of Canada (Hamilton 1971a, 1981). The oldest Fulgoromorpha are *Surijokocixius* from the U. Permian and *Boreocixius* from the L. Triassic of Siberia, and *Tricrosbia* (J. W. Evans 1971a) from M. Triassic of Australia. Fulgoridiidae are known from the Jurassic of Eurasia, Cixiidae from the L. Cretaceous of England (Fennah 1961) and Ricaniidae from the Palaeocene of Dakota (U.S.A.). A review of

achenorrhynchan phylogeny was given by Shcherbakov (1988b).

HETEROPTEROID GROUP (= COLEORRHYNCHA + HETEROPTERA) (U. Permian–Recent). Heteroptera share with Coleorrhyncha a number of features, including a long CuA, atrophied CuP, and a ‘Y vein’ (in the clavus) which ‘crosses’ the claval furrow and fuses with CuA₃₊₄ (synapomorphies) (Wootton 1965). Peloridiidae (Fig. 6.25j), the only extant Coleorrhyncha, have an arched CP₃₊₄ as in Auchenorrhyncha, retain an independent ScP (as in primitive Heteroptera; Fig. 6.25k) and have a triangular area antero-basally to ScP (as in the extinct Glosselytrodea). The Jurassic Karabasiidae from Siberia are related to living Peloridiidae (Popov 1985). Progonocimicidae (= Actinoscytinidae) (U. Permian–L. Cretaceous) (Fig. 6.25k) are the earliest occurring heteropteroids (Wootton and Betts 1986), with nearly homopteroid venation; they may belong to the Hemiptera stem group (Popov 1985) and are considered by Popov and Shcherbakov (1988) to be directly ancestral to Peloridiidae. Evolution of the wing venation was studied by Szelegiewicz (1971) and Szelegiewicz and Popov (1978). The groundplan of heteropteroids, as proposed here, contains a long ScP- (not supporting R as in Auchenorrhyncha; symplesiomorphy of Heteroptera, Coleorrhyncha and Glosselytrodea) and a reduced CuP (apomorphies). Early Heteroptera fossils belong primarily to the Nepomorpha, which became fully diversified by the Jurassic (Popov 1971). Triassicoridae from the M. Triassic of Australia belong at the base of this group, and Archegocimicidae (U. Jurassic of Karatau) belong to the related Leptopodomorpha. Nepidae, Belostomatidae, Corixidae, Naucoridae and Notonectidae are all recorded from the Jurassic (England, Germany, U.S.S.R., U.S.A.). Among the Cimicomorpha, Miridae have been recorded from the U. Jurassic of Karatau. Pentatomomorph fossils include Aradidae from the U. Cretaceous of Siberia (Kormilev and Popov 1986), Alydidae from the U. Jurassic of Karatau, and possible members of the group from the L. Jurassic of Germany. A review of the rich Jurassic and L. Cretaceous fauna from Mongolia and Siberia was published by Popov (1980, 1985, 1986). [Popov and Wootton 1977; Dolling, Popov, Whalley unpubl.]

Endopterygota

(U. Carboniferous–Recent). Endopterygota probably have an ancient, sister-group relationship with hemipteroids (Hennig 1981). Both groups share the following features: M forked immediately at base (symplesiomorphy), MA fused with R (synapomorphy, also in blattoid assemblage) and a brace (cross-vein or fusion) present between MP and CuA (synapomorphy). In immature endopterygotes the wing buds (which develop externally in all other pterygotes) became invaginated, probably in association with a desclerotised cuticle. The abdominal triangular sternum in the groundplan of Insecta was preserved (Fig.6.3b). A cryptosternum (invaginated meso- and metasternum) is common in the group. The coxae

acquired an additional ventral condyle articulating with the sternum (base of furca). Up to 3 pairs of leg-derived, abdominal appendages (leglets, CX and TR endites) are retained in some modern embryos, with TR endites serving as pleuropodia. Eruciform, polypod larvae retain functional abdominal leglets. Recent aquatic, ‘oligopod’ larvae (e.g. of Megaloptera) use filamentous leglets as gills and CX endites as gill clusters. The oldest known endopterygote larva (Fig. 6.26A), from Westphalian D (U. Carboniferous) of Illinois, has primitive, long antennae, ocelli, probably compound eyes, a dicondylous jaw, leg-like maxillary palps, annulated cerci and segmented abdominal leglets; legs and leglets bear double claws, showing that modern ‘prolegs’ are leg homologues. Endopterygote wings are homonomous, folded at first roofwise (at least in the groundplan) and only along the jugal fold, and covered by setae (all of which occur in hemipteroids, the last two unique in Pterygota). In the fore wing, MA is fused with R and diverges again, either from R or from RP (also seen in blattoids). ScA+ is weak and oblique, and it is sometimes transformed into a bulge. In the fore and hind wings, the base of AA fuses for a short distance with CuP; in derived forms AA₁₊₂ fuses completely with CuP. PC survived in Coleoptera (and Auchenorrhyncha) in the form of an epipleuron. A cutting, striated ovipositor and short cerci occur both in Palaeozoic endopterygotes and hemipteroids.

Two endopterygote lineages are recognised: (1) Mecopterida + Hymenoptera [head orthognathous, without a gula (primitive); larva eruciform, polypod] and (2) Coleopterida + Neuropterida [head prognathous with gula; larva campodeiform, ‘oligopod’]. Carboniferous endopterygotes are difficult to separate from some early

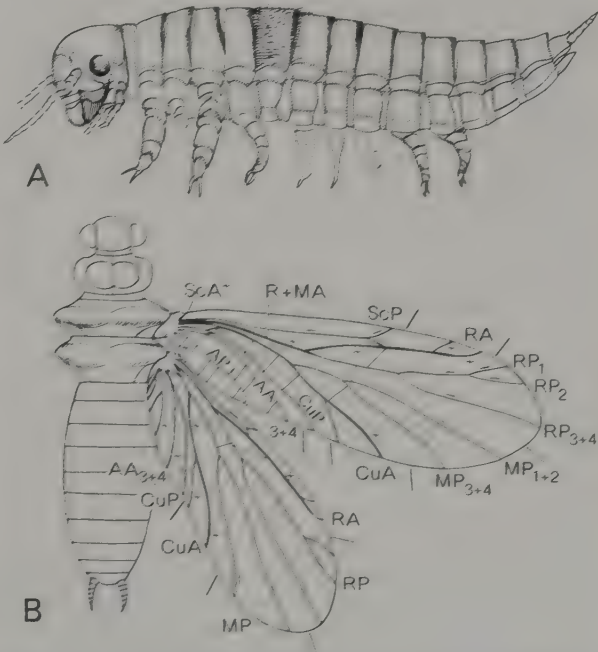


Fig. 6.26 A. Oldest known endopterygote larva, U. Carboniferous of Illinois, U.S.A.; B. Miomoptera: *Delopterum sinuosum*, L. Permian of Moravia. [J. Kukalová-Peck]

hemipteroids because the only reliable character, a ventral condyle on the coxa, is rarely preserved.

Mecopterida

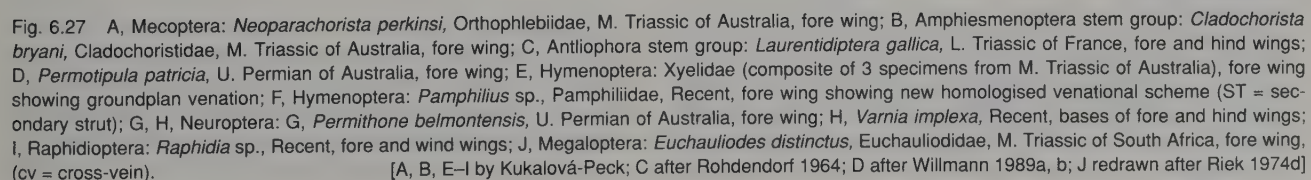
(Permian–Recent). The Mecopterida (= Panorpoidea of Hinton 1955b; Mecopteroidea of Kristensen 1975, Willmann 1987) are probably the sister group of the Hymenoptera (Hennig 1981). The Permian and Triassic fossil record contains a great diversity of Mecoptera-like endopterygotes, including the stem groups of Mecopterida + Hymenoptera, Mecopterida, Amphiesmenoptera (Trichoptera + Lepidoptera) and Antliophora (Mecoptera, Diptera and Siphonaptera), together with early members of Recent orders. Many of the fossils discussed under the extant orders actually belong to these basal assemblages or stem groups. As proposed here, the groundplan venation shares with Hymenoptera a narrow costal area and MA diverging from RP (apomorphies). Primitive features retained include CP- and ScA+ very short and oblique, ScP with serial branches (seen often in fossils), and MP basally adjacent to, but not fused with R. CuA is always braced with MP (an endopterygote apomorphy), primitively by a highly convex secondary strut (sometimes erroneously called 'M₅') or by fusion. AA₁₊₂ is fully fused with CuP (apomorphy). All immediate ancestors of the Mecopterida (Antliophora and Amphiesmenoptera) already have a venational groundplan with a conspicuously simplified wing venation (Willmann 1987, 1989a). All enrichment in branching and cross-veins within these lineages occurs only in the more derived subgroups, as a secondary autapomorphic trend [e.g. numerous ScP branches in the costal area of some Mecoptera (Meropeidae, Eomeropidae) and some Recent Trichoptera]. Thus, isolated Palaeozoic wings of the 'mecopteroid' type with richly branched primary venation and subcostal branches cannot be classified within the Mecopterida.

MP₄ fuses with CuA₁₊₂ in all Mecoptera (Fig. 6.27A) and all Diptera. In Trichoptera and almost all Lepidoptera (not in the Recent *Agathiphaga*) a simple CuA is connected to MP₄ by a cross-vein (but additional secondary branches on CuA can develop). The anal veins formed loops after they became connected by cross-veins and subsequently lost the posterior sections in Trichoptera and Lepidoptera, and by convergence, also in Permeropidae and Protomeropidae (= Platychoristidae) (which probably belong to the stem group of Hymenoptera + Mecopterida), as well as in primitive Hymenoptera (Kukalová-Peck and Willmann 1990). In the hind wings of many mecopterids, the bases of AA₃₊₄ and CuP are adjacent or fused for a short distance and a convex fold runs just in front of CuA. Members of the Mecopterida or Antliophora stem group include Permeropidae and Lithopanorpidae (L. Permian); Mesochoristidae and Agetopanorpidae (L. Permian–Jurassic); Martynopanorpidae, Belmontiidae ('Paramecoptera') and Petrochoristidae (U. Permian); and other families. 'Protomecoptera' from the Permian of the Kuznetsk Basin, belong to a basal assemblage outside of the mecopterids (Willmann 1987).

Miomoptera (U. Carboniferous–L. Jurassic). Common, mostly small (9–16 mm wingspan), with short bodies, long wings and simplified venation (Fig. 6.26B). Possibly belonging to the mecopterid-hymenopterid stem group. MP and CuA in both wings partially fused. In the hind wing, the base of AA₃₊₄ is fused to CuP (as in many mecopterids), but the CuA branches are not fused with MP₄. The long-disputed Carboniferous *Metropator pusillus* bears some mecopterid features (Tillyard 1935a), and probably represents a miomopteran hind wing (Carpenter 1965). Palaeomanteidae occur in the late U. Carboniferous of Germany and France and are most diverse and abundant in the warm temperate L. Permian of Moravia, Czechoslovakia (Kukalová 1963). Palaeomantiscidae lived in the L. Permian of Ural Mts (Rasnitsyn 1977); Permosialidae in the Permian of South Africa, Europe, U.S.S.R. and Asia and in the Triassic of Central Asia and South Africa (Riek 1976c).

Antliophora and Mecoptera (Permian–Recent). The venation of the Palaeozoic, antliophoran stem group, ancestral Mecoptera and ancestral Diptera often cannot be distinguished from each other. In all the ScP branches are lost and CuA₁₊₂ is fused with M₄ (both derived features). CuA₁₊₂ and M₄ are incompletely fused in some fossils, e.g. *Neoparachorista splendida* from the Australian U. Triassic (Riek 1955g), and in the Recent *Chorista australis*. The wings of Mecoptera and Diptera also lack the anal loops which developed in Trichoptera and Lepidoptera. The mecopteran groundplan venation has no subcostal branches, ScP is forked, RP and MP have four main branches, and MP is braced with CuA by a convex strut (a cross-vein erroneously called by some 'M₅' [Kukalová-Peck and Willmann 1990]) or by temporary fusion (Fig. 6.27A). Robinjohniidae, known from the U. Permian (Australia), may be closely related to the extant Nannochoristidae; if the two groups were combined, then Nannochoristidae would be the oldest surviving insect family (Riek 1976c; Willmann 1984, 1987). Undoubted Nannochoristidae occurred in the U. Permian of Australia and the L. Jurassic of Siberia (Sukacheva 1985a). The extinct Xenochoristidae, Triasochoristidae and Mesopanorpididae are known from the M. Triassic of Australia, and the last family occurred during the same period in South Africa. The extinct Neorthophlebiidae and Orthophlebiidae (Fig. 6.27A) occurred in the Triassic and Jurassic (Sukacheva 1985a). Bittacidae first appeared in the Jurassic and Choristidae in the L. Cretaceous. The first Eomeropidae (a family now restricted to South America) were found in the Jurassic of Kirgizia (Ponomarenko and Rasnitsyn 1974). The genus *Eomerope* occurred in the L. Tertiary of the U.S.A. and U.S.S.R. (Carpenter 1972; Ponomarenko and Rasnitsyn 1974). A nannochoristid larva and adults of Choristidae and other families are known from the L. Cretaceous of Vic. (Jell and Duncan 1986). Willmann (1987, 1988) presented a phylogeny of the Mecoptera.

Diptera (Triassic–Recent). The Diptera are the closest relatives of Mecoptera. Diptera have petiolate fore wings with derived, simplified venation in the groundplan with ScA oblique and straight; ScP shortened, R and RA



straight; RP twice dichotomously branched; MA fully fused with R. The convex 'spurious vein' between RP_{3+4} and MP_1 is a secondary intercalated sector on the crest of a flight-induced medial fold. Base of MP reduced then MP met simultaneously by CuA and arculus (r-mp cross-vein); MP + CuA fusion short. MP divides into MP_1 , MP_2 and MP_3 , while MP_4 is probably fused with CuA_{1+2} ; Cu is stemmed. The concave 'CuP' close to CuA is a secondary vein. CuP (= 'A₁') is shifted distally away from CuA; cua-cup cross-vein short. CuP- is superimposed by AA_{1+2+} basally. Anal veins are restricted to AA_{3+4} and AP_{1+2} . *Laurentidiptera gallica* (Fig. 6.27c), formerly referred to as 'Paratrichoptera' (Rohdendorf 1964) from the L. Triassic of France, and *Pseudopolycentropus* from the U. Jurassic of Karatau and L. Jurassic of Europe, have a fully developed CuP and small hind wings and possibly belong to the Antliophora stem group. The oldest true fly *Permotipula patricia* (Willmann 1989b) and the four-winged 'Protodiptera', *Permotanyderus* and *Choristotanyderus* (Riek 1977b) which are related to Diptera, are all from the U. Permian of Australia. The well-advanced bibionomorphous *Crosaphis* (Crosaphididae, near the ancestors of Mycetobiidae) is known from M. Triassic of Australia (Kovalev 1983). Recent families occur in the L. Jurassic of Issyk-Kul (Rohdendorf 1964). Many Jurassic Diptera from Siberia were described by Kalugina and Kovalev (1985) and numerous Mesozoic and Tertiary Diptera by Hennig (see Hennig 1981). Recent families of Nematocera, Orthorrhapha and Cyclorrhapha occur in the L. Cretaceous of Vic. and Transbaikalia (Kalugina 1989); Cyclorrhapha also occur in Lebanese Cretaceous amber. All families of Phoroidea are known since the U. Cretaceous. The first muscoid and bibionid flies are from the Canadian U. Cretaceous (J. F. McAlpine 1970; Peterson 1975). A bot fly was found in the stomach of a Siberian mammoth (Grunin 1973).

Siphonaptera (L. Cretaceous–Recent). Fleas probably emerged from the mecopterid stem group early during the Carboniferous, and they retained the primitive, leg-like labial palps (with up to 5 segments) which do not occur in the groundplan of the Mecopterida. *Niwratia elongata* (family uncertain) from the L. Cretaceous of Vic. had a typical siphonapteran body, including a pronotal comb, but had long slender legs. Two Pulicidae and *Tarwinia australis* (probably also a flea with thin legs) occurred in the same deposits (Jell and Duncan 1986). *Saurophthirus* and *Saurophthiroides* (Saurophthiridae) from the L. Cretaceous of Transbaikalia and Mongolia, respectively, might have been flea parasites of flying reptiles (Ponomarenko 1976, 1986). *Palaeopsylla* is a hystrihop-syllid from Eocene Baltic amber.

Amphiesmenoptera (Permian–Recent). The stem group of the Trichoptera and Lepidoptera had looped anal veins (apomorphy, originally weakly expressed; convergent with Protomeropidae and Permomeropidae) and a simple CuA, linked with MP_4 by a cross-vein. The fork on CuA in living Amphiesmenoptera probably represents a derived condition (Willmann 1989a). Some Recent Trichoptera have developed secondary ScP branches (autapomorphy). Permomeropidae and Protomeropidae

from the L. Permian of Moravia, Czechoslovakia (Kukalová-Peck and Willmann 1990). Kansas, and the Ural Mts and Kuznetsk Basin (Permotrichoptera of Sukacheva 1976) are not Mecopterida but may belong to the Mecopterida-Hymenoptera stem group (Willmann 1989a). The earliest Amphiesmenoptera are possibly the L. Permian *Microptysmella* from Moravia (Kukalová-Peck and Willmann 1990) with incompletely expressed loops and a simple CuA, but microptysmatids from the L. and U. Permian of the U.S.S.R. (Kuznetsk Basin and Ural Region) have perfect loops. The Cladochoristidae (Fig. 6.27a) from the U. Permian of Australia and Triassic of Kirgizia have secondary ScP branches (Willmann 1989a).

Trichoptera (Triassic–Recent). The Triassic of Kirgizia produced Philopotamidae, Prorhyacophilidae and Necrotauliidae (Sukacheva 1973, 1982). Jurassic Trichoptera occurred in southern Siberia and western Mongolia (Sukacheva 1985b). Recent trichopteran families probably have existed at least since the Jurassic (Hennig 1981). Integripalpi caddis cases are known since the L. Cretaceous. Leptoceridae and a calamoceratid pupa occurred in the Cretaceous of Vic., and various Cretaceous caddis-flies are known from Transbaikalia and Taimyr, U.S.S.R., Canada, and Tennessee, U.S.A. Caddis-flies are common in the Tertiary amber of the Baltic, Burma, Dominican Republic and Mexico (Chiapas) (Botosaneanu and Wichard 1983). The so-called 'Paratrichoptera', with Mesopsychidae from the Triassic of Australia and U. Jurassic of Central Asia, belong to the mecopterid stem group and may be descendants of the U. Permian Belmontiidae (Willmann 1989a).

Lepidoptera (Jurassic–Recent). Butterflies and moths are the sister group of caddis-flies. The primitive (presumably Triassic) larvae probably fed on mosses while adults had functional mandibles and ate pollen, when angiosperms were absent. Lepidoptera, except Recent *Agathiphaga* (Common 1973), have CuA_{1+2} and MP_4 fused (parallelism). A long controversy concerns the alleged oldest moth from the M. Triassic of Australia, *Eoses triassica* (Tindale 1945); Sukacheva (1982) placed this wing fragment in Permochoristidae, while Willmann (1984) considered it to be a synonym of *Mesochorista proavita*. Also controversial is *Eocorona iani* (Tindale 1981), which could be either a lepidopteran or a trichopteran (Whalley 1986) and which may be congeneric with *Prorhyacophila* (Trichoptera) (Sukacheva 1982). The classification of *Mesoses* from the U. Triassic of Africa is uncertain. *Archaeolepis*, the oldest distinguishable lepidopteran, occurred in the L. Jurassic of England (Whalley 1986) and *Eolepidopterix* in the U. Jurassic of the U.S.S.R. (Rasnitsyn 1983a). Recent families probably differentiated in the Jurassic or earlier, but no record is available so far. L. Cretaceous Lebanese amber contains putative Incurvarioidea, and Microptergidae (*Parasabatinca*) (Whalley 1986). Various fragments of bodies, scales, noctuid eggs, etc. are reported from the Cretaceous of France, Siberia, Transbaikalia and Canada. The evolution of the Lepidoptera was discussed by Kozlov (in Ponomarenko 1988). Recent families are recorded from at least 200 specimens in the Tertiary. Butterflies and moths

were differentiated by the Cretaceous. Leaf mining occurs commonly in the U. Cretaceous (Zherikhin 1978). Recent species of some leaf miners have persisted since the Miocene (Opler 1973).

Hymenoptera

(Triassic–Recent). The sister group of Hymenoptera is possibly the Mecopterida (Hennig 1981). Hymenoptera and mecopterids share a relatively narrow costal area and MA fused with R and RP (not only with R as in primitive neuropterids [Fig. 6.27H]). However, the anal veins in the fore wing of Hymenoptera are uniquely derived from a very primitive condition, ancestral to Mecopterida. The hymenopteran groundplan venation is best represented in primitive Xyelidae from the U. Triassic of Australia (Fig. 6.27E): CP- and ScA+ are weak and oblique (the neuropterid bulge on ScA+ missing); the costal area has ScP branches (seen only in fossils), and MP diverges from R + M and immediately completely fuses with CuA (apomorphy of Hymenoptera); and MA is fused at base with R, remains fused to RP (synapomorphy with mecopterids) and separates from it as its proximal branch. AA₁₊₂ is almost completely free from CuP; this is an extremely primitive feature indicating an early divergence of Hymenoptera, probably well before the Triassic. A comparison of Figs 6.27E and F shows that AP₁₊₂ and AA₃₊₄ form, together with two cross-veins, the sinuate anal vein. In modern forms, the stem of Cu is short, while the base of CuA and the entire CuP are reduced (autapomorphy of Hymenoptera). In the hind wing AA and AP are long and simple; and JA and the jugal area are well developed.

The oldest fossils are Xyelidae from the M. Triassic of Australia and Central Asia (Rasnitsyn 1969, 1988a, b). Many Recent and fossil families occur in numerous Mesozoic and Tertiary localities, especially in the U.S.S.R. (Masner 1969a, b; Rasnitsyn 1969, 1975, 1980, 1983b, 1986a, b; H. E. Evans 1969a, 1973; Townes 1973; Douth 1973; Wilson 1985a, b; Yoshimoto 1975; Menke and Rasnitsyn 1987). Various siricomorphs and the first parasitic Karataviidae appeared in the Jurassic, followed by phytophagous ancestral tenthrinoids (Xyelotomidae), ancestral vespomorphs (Bethylonymidae), and parasitic forms, including Paroryssidae, Ephialtitidae, lower Evanioidea, Ceraphronoidea and Proctotrupoidea. Tenthredinidae, Ichneumonoidea, Cynipoidea, higher Evanioidea, Ceraphronoidea and Proctotrupoidea occur early in the Cretaceous, along with the aculeate Bethylidae, Chrysidae, Dryinidae, Sphecidae, Pompilidae, Scolidae and Vespidae; ants and Chalcidoidea occur later in the period (Rasnitsyn 1988b). Extinct Eoichneumonidae and Recent Aulacidae, Proctotrupidae and Sphecidae were found in the L. Cretaceous of Vic. (Jell and Duncan 1986). A species of Oligocene scelionid wasp (from Baltic amber) still lives unchanged in South Africa and Madagascar (Masner 1969a). Early Formicidae lacked features indicating sociality (Dlusskiy 1983). Ants are related to 'scolioid' wasps and occur in the U. Cretaceous of Lebanon, New Jersey, U.S.A. (Sphecomyrminidae) (Wilson *et al.* 1967), and Siberia (Armaniidae,

Sphecomyrminidae) (Dlusskiy 1983). Many ants are known from Baltic and Dominican amber (Wilson 1985a, b; Baroni Urbani and Wilson 1987). The early evolution of ants was examined by Dlusskiy and Fedoseeva (in Ponomarenko 1988). Ant abundance reached its present level in two steps: in the Eocene with Dolichoderinae and Formicinae, and in the Miocene with Myrmicinae and Formicinae (Rasnitsyn 1988b). The oldest honey bee was found in the Oligocene of the Indian subcontinent (Culliney 1983). Phylogenies of the Hymenoptera have been proposed by Rasnitsyn (1975, 1980, 1983b, 1988a) and Zessin (1985).

Neuropterida

(Permian–Recent). The neuropterid orders (Neuroptera, Raphidioptera and Megaloptera) have in the groundplan a broad costal area (a primitive feature, seen also in the blattoid assemblage) with CP- short; a conspicuously bulging ScA+ (a neuropterid apomorphy); ScP terminating on the costal margin (primitive); MA separating from R (Fig. 6.27H) (not from RP, as in Mecopterida and Hymenoptera) as a convex branch, but later captured into the RP system (Fig. 6.27G); MP- not fused with R; shallow claval furrow proximal to CuP (a neuropterid apomorphy); in the hind wing, CuP running at the bottom of the claval furrow (primitive) and later tending to become reduced (neuropterid autapomorphy).

Neuroptera (Permian–Recent). Possibly the sister group of Raphidioptera + Megaloptera. The groundplan venation has pectinate RP branches (apomorphy), but is primitive in having richer branches and cross-veins (this pattern is secondarily enriched in some neuropterans). In the fore wings MA diverges from R as in the neuropterid groundplan (Fig. 6.27H), but later joins the RP system by means of a cross-vein (Fig. 6.27G) (autapomorphy). In the hind wings, MA separates from the stem of RP and AA₁₊₂ is fused only shortly with CuP (extremely primitive). Many of above mentioned, primitive features are preserved in the living *Varnia implexa* (Ithonidae) from Vic. (Fig. 6.27H).

The oldest (undescribed) Neuroptera occur in the L. Permian of Moravia, Czechoslovakia. The U. Permian of the Ural Mts and Kuznetsk Basin has yielded Sialidopsidae, Palaeomerobiidae, Permithonidae (Fig. 6.27G), Permopsychopidae and Archeosmylidae, the ancestors of Osmylidae. The last three families also occur in the Permian of Australia and Palaeomerobiidae also in South Africa and Siberia (Riek 1976c). The rich M. Triassic fauna of Australia has yielded Osmylopsychopidae, Mesoberothidae, Proberothidae, Archeosmylidae and Osmylidae. In the Jurassic of Solenhofen, Germany, and England, Recent families are found together with Prohemerobiidae, Osmylopsychopidae, the gigantic, butterfly-like Kaligrammatidae, Permithonidae, Mesopolystoechotidae and Brongniartiellidae (Whalley 1988b). The U. Jurassic Mesochrysopidae from Bavaria, Germany and Kazakhstan may represent the stem group of Chrysopidae. Jurassic forms from Siberia and western Mongolia were described by Ponomarenko (1985). Coniopterygidae are known from the U. Jurassic of

Kazakhstan, the Cretaceous of Lebanon (Whalley 1980), Taimyr (U.S.S.R.) and the Eocene Baltic amber (Meinander 1975). Ascalaphidae, Nymphidae and Psychopsidae occur in Eocene Baltic amber (MacLeod 1971); and Osmylidae have been recorded from the Palaeocene of Australia (Lambkin 1987).

Raphidioptera (Jurassic–Recent). As the sister group of Neuroptera, Raphidioptera + Megaloptera share the impoverished cross-venation and the separation of MA from RP in the fore wing (synapomorphies). Raphidioptera retain a dichotomously branched RP (Fig. 6.27i) and have venation and cross-venation richer and more primitive than in Megaloptera, with MA+ in both wings distinctly convex. Mesoraphidiidae and Baissopteridae are known from the Jurassic and L. Cretaceous of Asia and Europe, and Alloraphidiidae occurred in the U. Cretaceous of Labrador (Carpenter 1968). All alleged pre-Jurassic occurrences have been questioned. The two Recent families are known from Eocene Baltic amber and from the Miocene of the U.S.A.

Megaloptera (Permian–Recent). Megaloptera are the sister group of Raphidioptera and have the most derived and simplified venation of all neuropterids. RP is pectinate and MA+ in the fore wings is no longer discernible (Fig. 6.27j). In the hind wings of Megaloptera and Raphidioptera, a convex brace between MP and RP is not MA+, but a cross-vein (Achtelig, in Hennig 1981). Recent embryos and aquatic larvae preserve up to 3 pairs of leg-derived appendages on abdominal segments (leglets, coxal and trochanteral endites) (Kukalová-Peck 1988a). U. Permian Megaloptera (Parasialidae from Arkhangelsk and Tychtodelopteridae from Kuznetsk Basin) were revised by Ponomarenko (1977). Euchauliodidae (Riek 1974d; Fig. 6.27i) are known from the U. Triassic of South Africa and Corydalidae with lacustrine larvae, from the L. Cretaceous of Siberia. The U. Cretaceous larva, *Chauliosialis*, shows some sialid features. Most Palaeozoic and Mesozoic larvae probably inhabited oxygen-rich, mountainous streams which left few fossiliferous sediments. Modern genera are known from Eocene Baltic amber and from the Miocene of the U.S.A.

Coleopterida

(Permian–Recent). Beetles and their possible sister group Strepsiptera (see below) have common ancestors with the neuropterids (Kristensen 1981; Lawrence and Newton 1982). They diverged by developing convex, sclerotised, non-flying elytra probably adapted to sealing the body from dessication and protecting it from predators by widening the ancient precostal area of the proto-wing into an epipleuron. A short epipleuron also occurs in some Auchenorrhyncha, which inhabited with beetles the cold habitats of Gondwana and Angara. Divergence of beetles must have taken place before the precostal veinal pair merged irreversibly with the costal margin, a process vital for a flightworthy wingblade (that is, at an early stage in flight adaptation). As interpreted here, the most complete, primitive coleopterid venation may be present in the elytra of Ademosynidae (Fig. 6.28A), where CP- and ScA+

are very long (apomorphy), RA and RP are separate (very primitive), RP and MA completely fused (apomorphy), CuP- is fused with AA₁₊₂, AP is concave (very primitive) and JP- has a long fork (apomorphy). The elytral venation of Palaeozoic Tshekardocoleidae (Figs 6.28B, C) has primitive cross-venation but is derived and impoverished in having a reduced ScA, largely fused CP- and ScP-, CuP + AA₁₊₂ reduced to a shallow groove, and JP having one branch only. Hind wing venation in modern Coleoptera can be derived from the common neuropterid-coleopterid ancestor and not from the already specialised, convergently impoverished megalopteran system, as is sometimes claimed. It has a precostal strip (homologous with the elytral epipleuron) still visible in some forms, RA diverging from RP close to the base (very primitive for Neoptera) and a claval fold with CuP reduced as in neuropterids. The interpretation of the veinal pattern is discussed in Chapter 35. The hind wings of true Coleoptera share the following synapomorphies: 1) RA and RA₁₊₂ are combined with and strengthened by ScP into a stiff bar, which also forms the anterior limit of the radial cell (in Archostemata and Polyphaga) or at least partly enters the pterostigma (Adephaga and Myxophaga). 2) The radial cell (homologous with the neopterous pterostigma) is always present between RA₁₊₂ and RA₃₊₄ as an apomorphy of the order; RA₃₊₄ delimits the radial cell posteriorly in Archostemata (Fig. 35.5A) and proximally, posteriorly and distally in Polyphaga (Figs 35.5F, G); in Adephaga and Myxophaga, the radial cell is delimited posteriorly by RA₃₊₄ and distally partly by RA₃ (Figs 6.28E, 35.5C) (plesiomorphy). 3) MP₁₊₂ becomes associated with the end of RP to form a medial loop (see Chapter 35). Ponomarenko (1972) described the hind wing of an U. Permian coleopterid which lacks the apomorphic features of the order Coleoptera mentioned above; this probably represents an independent derivative of the coleopterid stem group. A different veinal interpretation consistent with that used for Coleoptera is shown in Fig. 6.28D.

Protocoleoptera (Permian–?Triassic). The oldest known beetle-like fossils are members of the family Tshekardocoleidae (Figs 6.28B, C) from the L. Permian of Moravia, Czechoslovakia, and the Ural Mts, U.S.S.R. These were placed in the suborder Protocoleoptera by Crowson (1975) and are here considered to belong to the coleopterid stem group. They had elytra resembling modern Cupedidae with a derived veinal pattern but had primitive cross-veins, a long outer ovipositor, a short abdomen which did not fit tightly against the elytra, 13-segmented antennae and other non-coleopterous features (Crowson 1975; Lawrence and Newton 1982). Permian fossils are often difficult to classify, especially when they consist of isolated elytra. They were all included in the suborder Archostemata by Ponomarenko (1969b), who recognised several additional families (e.g. Taldycupedidae, Asiocoleidae, Permocupedidae, Rhombocoleidae) and two 'parataxonomic' assemblages, Schizocoleidae (elytra with an interlocking device) and Permodynidae (striate elytra). Crowson (1975) proposed another suborder Archecoleoptera for those Upper

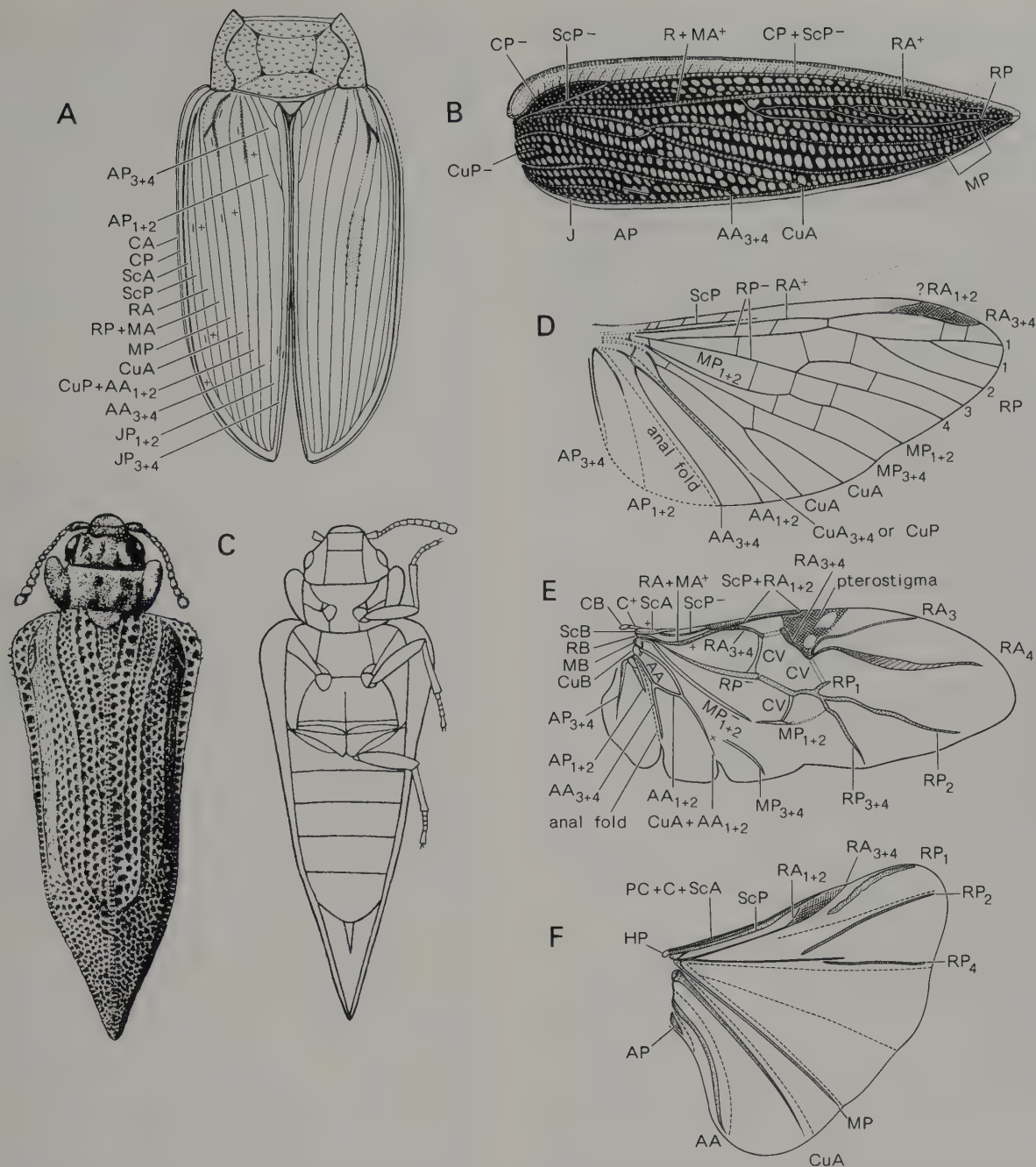


Fig. 6.28 Coleoptera: A, *Ademosyne speciosa*, Ademosynidae, U. Triassic of South Africa, prothorax and elytra showing the complete venational system; B, *Votocoleus submissus*, Tsherkardocoleidae, L. Permian of Moravia, elytron showing reduced and fused venation; C, *Sylvacoleus sharovi*, Tsherkardocoleidae, L. Permian of Ural Mts, U.S.S.R., dorsal and ventral; D, Primitive coleopterid hind wing, U. Permian, Ural Mts, U.S.S.R. (new interpretation); E, *Haliphus* sp., Haliplidae, Recent, hind wing showing newly homologised venational system; F, *Coriophagus rieki*, Strepsiptera, hind wing (new interpretation). [A, D, E, F by Kukalová-Peck; B after Kukalová 1969a; C after Ponomarenko 1969b]

Permian forms which were intermediate between tsherkardocoleids and true Archostemata, but no clear distinguishing characters were given. The Permian fossils probably contain representatives of several related orders comparable to the taxa comprising the mecopterid assemblage, coexisting with primitive beetles at least in the U. Permian. We have chosen to place them in a single paraphyletic group.

Coleoptera (Upper Permian–Recent). Changes between

the stem group assemblage and true Coleoptera included: 1) decrease in the number of antennal segments to 11; 2) development of more regular, subparallel elytral ribbing; 3) elongation of the abdomen (or shortening of the elytra) so that the two became coadapted; 4) invagination of the external ovipositor; 5) modifications of ScP, RA and the pterostigma into the radial loop (as discussed above) and of MP and the tip of RP into the medial loop in the hind wing. Triassic beds of Central Asia contain a large

number of Archostemata (Cupedidae and Ommatidae), as well as the first Trachypachidae (Adephaga), the extinct cupedoid family Tricoleidae, the Ademosynidae, which may be near the base of Polyphaga, the extinct adephagan family Triaplidae, and many Catiniidae and Schizophoridae, including forms which may have been ancestral to the Myxophaga. In addition, the first undisputed Polyphaga (*Peltosyne*) and undescribed Elateriformia and Curculionoidea occur in these deposits. The Jurassic and Cretaceous faunas of the U.S.S.R. and western Mongolia are particularly rich, and include a number of extinct families (e.g. adephagan Coptoclavidae, Liadytidae, Parahygrobiidae and Jurodidae; and polyphagan Praelateridae); members of the extant families Dytiscidae, Hydraenidae, Hydrophilidae, Staphylinidae, Elateridae, Cerophytidae, Trogossitidae, Nitidulidae, Mordellidae, Cerambycidae, Chrysomelidae, Nemonychidae and Attelabidae; basal Staphylinoidea (*Mesecanus*) and Scarabaeoidea; and a number of cleroid and cucujoid taxa of uncertain relationships (Arnoldi, Ponomarenko, Nikritin and Zherikhin in Arnoldi *et al.* 1977; Dolin 1973, 1975; Ponomarenko 1973, 1980, 1986, 1987; Ryvkin 1985; Tikhomirova 1968). A Jurassic elytron has been found in Antarctica (Tasch 1973). Dytiscidae, Gyrinidae, Hydraenidae, Hydrophilidae, Staphylinidae, Pselaphidae, Scirtidae, Cantharidae and Mordellidae occur in the L. Cretaceous of Vic. (Jell and Duncan 1986). Labradoroleidae are known from the Cretaceous of Labrador (Ponomarenko 1969a). Kuschel (1983) commented on the phylogenetic relationships of fossil Curculionoidea, based mainly on Jurassic and Cretaceous material from the U.S.S.R. (Arnoldi *et al.* 1977). Recent genera are abundant in the Tertiary and especially in Quaternary bog deposits of the Northern Hemisphere. Late Caenozoic Coleoptera are reviewed by Coope (1979), beetles in amber and copal by Spahr (1981).

Strepsiptera (L. Cretaceous–Recent). This possible sister group of Coleoptera (Kinzelbach 1971a; Kristensen 1981, and Chapter 5) retains some primitive characters, including the fore wings being capable of whirring (Kinzelbach, in Hennig 1981) and a well-delimited patella. Young larvae, at least, have invaginated wings (confirming their placement in Endopterygota) and adults use only hind wings in flight (a synapomorphy with Coleoptera). The hind wing of Strepsiptera (Fig. 6.28F) shares with that of Coleoptera two important synapomorphies: 1) a shortened RA forming a pterostigma between RA_{1+2} and RA_{3+4} , and 2) a sclerotised and shortened ScP entering the pterostigma (as in Adephaga, Fig. 6.28E). It also shares the plesiomorphous separation of RA and RP at the wing base, and RP branches supporting folds, a very long fork of MP and a reduced CuP (synapomorphies). Quite clearly, Strepsiptera venation can be derived only from a common ancestor with Coleoptera or from the coleopterid stem group. The wing venation has R fused basally with MA (as in other Endopterygota), a concave RP with 4 branches, a strong MP which is forked or simple, a simple, sometimes shortened CuA, a reduced CuP, a strong AA, often a strong AP and a short and simple J.

Elenchidae occur in L. Cretaceous amber of Lebanon and Miocene Dominican amber, while Mengeidae and Myrmecolacidae are recorded from Eocene Baltic amber. A larva of *Stichotrema* (Myrmecolacidae) is known from the Eocene of Germany (Kinzelbach and Lutz 1985). The group has existed perhaps since the Carboniferous.

THE AUSTRALIAN FOSSIL RECORD

Over 400 fossil species, distributed in 20 orders, have been described from Australian deposits ranging in age from the U. Carboniferous to probably the Pliocene. The origin of the Australian insect fauna was discussed by Riek (1971b).

Carboniferous. A species of Palaeodictyoptera from U. Carboniferous shales in Tas. (Riek 1976b) apparently lived in an unusually cold climate.

Permian. The earliest occurrence is in a rich, fine-grained chert of the U. Permian Newcastle Coal Measures of Belmont and Warner's Bay in N.S.W. (Tillyard 1926a–b, 1935b–d; Riek 1968a). The insect fauna is associated with a temperate *Glossopteris* flora and is different from that of the warmer Northern Hemisphere. There are no Palaeoptera except an undescribed protonate, no orthopteroids and only single species of Blattodea (in Tas.), Plecoptera and Glosselytrodea (Permoberothidae). However, there are four southern families of Protelytroptera (Fig. 6.20B) (Kukalová 1966), many Auchenorrhyncha (J. W. Evans 1956), several Psocoptera and three families of Neuroptera (Fig. 6.27G), a few Coleoptera and Trichoptera, and abundant primitive Mecopterida (Fig. 6.27D) (Riek 1953).

Triassic. The Mt Crosby bed of the U. Triassic Ipswich Series in Qld has yielded more than a thousand recognisable insects (Tillyard and Dunstan 1916; Tillyard 1918b, 1918c, 1921a; Tindale 1945; Riek 1955g). Cockroaches dominate, and Auchenorrhyncha (Figs 6.25F–I) (J. W. Evans 1956, 1961, 1971a), the oldest aphids (Fig. 6.25A) and certain Mecopterida (Figs 6.27A–C) (Riek 1955g), including Diptera (a well-advanced bibionomorph) are plentiful. There are smaller numbers of Heteroptera (Fig. 6.25K), Orthoptera, Neuroptera and Coleoptera, while Odonata, Paraplecoptera, Plecoptera and Hymenoptera are each represented by one or two specimens.

In the Denmark Hill fauna, from the top of the Ipswich Series (Tillyard 1917a–23b; Riek 1956), about half the fossils are Coleoptera, with the Blattodea and Auchenorrhyncha as the other important components. There are a few Orthoptera, Phasmatodea, Neuroptera and Mecoptera. The Odonata, Glosselytrodea, Paraplecoptera, Phasmatodea and Trichoptera are each represented by one or two specimens.

Beautifully preserved remains of wings at Brookvale near Sydney, N.S.W., have been found in a lenticular shale in the M. Triassic Hawkesbury Sandstone (Riek 1954b). The orthopteroid fauna is dominated by the gigantic titanopterid *Clatrotitan* (Fig. 6.18D), which had an unusual resonating area in the fore wing of the male. One common mecopteran (Riek 1950), a number of Auchenorrhyncha, and some Blattodea are represented.

The Wianamatta Shales near Sydney are of U. Triassic or possibly Jurassic age and have yielded beetle elytra, large orthopteroid wings, a mesoblattinid cockroach, a mecopteran and an auchenorrhynchan wing (Etheridge 1888).

In Tas., fossil insects occur in the New Town Coal Measures, Hobart (Riek 1962c) and in the Mt Nicholas Coal Measures, Fingal. They include *Triassoblatta* cockroaches, which are also common in the Triassic of Qld. A fragment of a large scytinopterid Auchenorrhyncha was obtained at Hobart. Beetle elytra and a mesoblattinid cockroach have been collected at Hill River in W.A. (Riek 1968b).

Jurassic. *Griphologus lowei* from the Talbragar fish beds near Mudgee, N.S.W., was originally described as a cicada but placed by Handlirsch (1906–1908) among the groups of uncertain position.

Cretaceous. Two hind wings of the Mesozoic dragonfly family Aeschnidiidae are known from the marine limestones of the Flinders River beds in North Qld (Tillyard 1917b; Riek 1954c). There is an abundant insect fauna in the freshwater L. Cretaceous of Koonwarra, Korumburra Group, South Gippsland, Vic. It has yielded over 70 insects from 12 orders, mostly of living families. Species of Hemiptera, Coleoptera and Diptera prevail while ephemeropterans (Siphonuridae) and immature dipterans are abundant. Odonata, Blattodea, Plecoptera, Orthoptera, Psocoptera, Siphonaptera, Mecoptera, Trichoptera and Hymenoptera are lesser components (Jell and Duncan 1986).

Tertiary. In the L. Tertiary at Redbank Plans and Dinmore, South-East Qld, the insects are predominantly Auchenorrhyncha and Coleoptera, but a few Blattodea, Heteroptera, Neuroptera, Mecoptera and Diptera, an

orthopteran wing, Isoptera, a cicada and a wing fragment of an anisopteran dragonfly have been found (Riek 1952). Kauri (*Agathis*) resin with insect inclusions was found in the U. Tertiary of Vic. (Hills 1957).

The insects at Vegetable Creek near Emmaville in northern N.S.W. are in the youngest Tertiary, stanniferous lode of the field and are mostly well-preserved immatures of Ephemeroptera (Leptophlebiidae and Baetinae) and chironomid Diptera (Riek 1954a).

At Duaringa in Central Qld, two presumably Tertiary zygopteran dragonfly nymphs (Lestidae) were obtained from a bore core. In Vic., a few insect remains, mainly beetle elytra, are known from several localities.

Pleistocene insect fossils, especially beetles, have been abundantly reported in the Northern Hemisphere, mostly from peat deposits, but are not yet known from Australia. Quaternary copal inclusions and insect remains such as chironomid larvae from various lake sediments have potential for reconstructing environmental changes.

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Biogeography

P. S. CRANSTON *and* I. D. NAUMANN

Every taxon, of whatever rank, occupies a particular area of the globe, termed its *distribution*, *range* or *area of endemism*. This area of distribution need not be continuous, but may be *discontinuous* or *disjunct* and within its range a taxon may be scarce or abundant, permanent, seasonal or ephemeral. Furthermore, distributions may change over shorter or longer periods of geological time as ranges expand, contract or shift or, increasingly, when human activity has caused extinction or redistribution. The elucidation of where contemporary species occur is descriptive natural history or *faunistics* and *floristics*. The survey of historic biota is called palaeofaunistics and palaeofloristics, with an important subdiscipline of palynology, the study of fossil pollens.

Faunistic and floristic studies reveal that distributions are not random but are often strikingly congruent between quite unrelated taxa. For example, many taxa like those shown in Figs 7.1A–C are restricted or *endemic* to south-western Australia. Among the plants alone over 80% of all species occurring in the south-west are not represented elsewhere. Thus this region is considered to be an area of high endemism. When the flora and fauna are examined on a broader scale it emerges that the entire Australian continent together with Tasmania, New Guinea and some adjacent islands comprises an area of endemism exemplified by, among many others, *Eucalyptus* trees, morabine grasshoppers and monotreme mammals. It is possible therefore to see the globe as comprising nested sets of areas of endemism. The number of major regions of distinctive endemism (*biogeographic regions*) recognised by scientists has varied from 20 (Candolle 1820), to 40 (Candolle 1838), to six (Sclater 1858; Wallace 1876). The

six regions widely recognised today (Fig. 7.2) are those elaborated by Sclater and Sclater (1899), namely the Nearctic, Palaearctic, Neotropical, Oriental, Australian and Afrotropical (formerly Ethiopian) regions. From the earliest discussions of biotic regions, Australia has been recognised as distinctive, although views on other parts of the south-western Pacific, such as New Zealand and New Caledonia have been less consistent.

Faunistics and floristics in combination with recognition of areas of endemism, explanation of their genesis, and interpretation of the inter-relationship of faunas and floras and the areas they occupy is called *biogeography*. This discipline not only unites biology with geography and geology but is strongly linked to ecology.

This chapter considers the distinctive nature of the distributional patterns of the Australian biota, the different approaches to biogeographic analysis and the changing views of the origins and affinities of the biota.

The Discovery of Australian Biotic Distribution Patterns

The flora and fauna (including the insects) of Australia were noted to be unique from the time of their 'discovery' by European naturalists (see Chapter 8 and references therein). The first attempt to explain this uniqueness was that of Joseph Hooker, the botanist on the Ross voyages to Antarctica and the southern continents between 1838 and 1843. Hooker visited Tasmania, eastern Australia, New Zealand and the antarctic and subantarctic islands of Kerguelen, Campbell, Auckland, Cockburn, Falkland and those off Tierra del Fuego. Hooker's breadth of knowledge, derived from field experience which has hardly



been surpassed since, led him to recognise strong resemblances between the austral floras. He viewed this as representing the 'remains of a flora that had once spread over a larger and more continuous tract of land than now exists.' (Hooker 1853: p. xxi).

However, in his later introduction to the *Flora of Tasmania*, Hooker (1860) considered the Australian flora to comprise three ecologically and taxonomically distinct elements. These elements comprised (i) an *autochthonous* (endemic) element of taxa found in temperate open forest, woodland and heath, mainly of xeromorphic plants, with the genera *Eucalyptus* and *Acacia* prominent; (ii) an *Indomalayan* element with south-eastern Asian affinities, found in tropical and subtropical monsoon and rainforest habitats, and (iii) an *Antarctic* element found in temperate, southern rainforest and alpine habitats, characterised often by the southern beech *Nothofagus*, and showing affinities particularly with the floras of South America and New Zealand. Hooker also recognised cosmopolitan plant groups, mostly herbaceous in nature and widespread within Australia. As observed by Truswell *et al.* (1987), these views of Hooker (1860) provided the basis for the so-called 'invasion theory' of Australian biogeography. This theory proposed that the continent had been colonised by separate invasions by non-indigenous floras and faunas, from different directions at different times. For the following hundred years, in botany at least, dispersal into Australia via various postulated 'land-bridges' was the paradigm, exemplified by the phytogeographic monograph of Burbidge (1960). Contrary views existed but were little heeded until increasing awareness of the mobility of continents allowed Hooker's earlier (1853) biogeographic views of the southern continents to be revived (e.g. Specht 1981; Barlow 1981).

Botanists, with their better documented distributions, led the field in biogeographical studies, although Erichson (1842), in one of the first works on the Australian insect fauna, made a remarkably perceptive, early assessment of the faunal elements comprising Van Diemen's Land (Tasmania). Subsequently, however, entomologists tended to follow the botanists and vertebrate biologists in espousing invasions rather than *in situ* processes to derive the Australian fauna (e.g. J. W. Evans 1959; Paramonov 1959). Entomological biogeographers such as Darlington (1961a-d, 1965) minimised the autochthonous elements while stressing the predominant northern origin of, for example, the Australian carabid beetles. Tillyard's (e.g. 1926c) views on insect fossils and the origin of the Australian insect fauna stand in contrast in their acknowledgment of endemic elements and in the predominantly southern origin proposed for many groups.

Although the data for insects and other arthropods are not as complete as those for plants and vertebrates, there are many recent analyses for Australia, and proximate areas such as New Guinea, New Zealand and New Caledonia, as well as other southern continents. Examples

Fig. 7.1 Distribution maps of: A, jarrah (*Eucalyptus marginata*) (after Hall *et al.* 1970); B, *Metaballus frontalis* (ORTH: Tettigoniidae) (after Rentz 1985); C, Humming frog (*Neobatrachus pelobatoides*) (after Cogger 1975).



Fig. 7.2 The zoogeographic regions.

[Modified after Wallace 1876]

of insect and other arthropod groups for which there are explicitly biogeographic analyses (with the geographical scope of these analyses) include: araneid spiders, southern continents (Platnick 1976), mygalomorph spiders, southern continents (R. J. Raven 1980); scorpions, Australia (L. E. Koch 1977); Thysanoptera, New Zealand–world-wide (Mound 1983); Ephemeroptera, southern continents (Edmunds 1972, 1981); Odonata, Australia (Watson and Theischinger 1984a); Austroperlidae (PLEC), Australia (Illies 1969); Notonemouridae (PLEC), Australia (Illies 1975); Eustheniidae (PLEC), Australia–southern continents (Zwick 1979a); Gryllidae (ORTH), Lord Howe I.–Norfolk I.–New Caledonia (Otte and Rentz 1985); Tettigoniinae (ORTH), southern continents (Rentz and Gurney 1985); Psocoptera, south-western Pacific (Thornton 1980); Peloridiidae (HEMI), Lord Howe I.–Australia (J. W. Evans 1967); Cicadoidea (HEMI), Indo-Pacific (Duffels 1986); Miridae (HEMI), Indo-Pacific (Schuh and Stonedahl 1986); Coccidae (HEMI), South America–Australia (Qin and Gullan 1989); Micropterigidae (LEPI), south-western Pacific (Gibbs 1983); Papilionidae (LEPI), Palaeotropical (Saigusa *et al.* 1982); Tortricidae (LEPI), New Caledonia (Horak 1985); Siphonaptera, southern continents (Traub 1972); Blephariceridae (DIPT), Australia (Zwick 1975, 1977b); Chironomidae (DIPT), southern continents (Brundin 1966), Western Australia–southern Africa (Cranston *et al.* 1987); Mycetophilidae (DIPT), world-wide (Munroe 1974); *Drosophila* (DIPT: Drosophilidae), Australia (Parsons and Bock 1981); Sepsidae (DIPT), Australia (Colless 1980); Derodontidae (COLE), Australia–New Zealand–Chile (Lawrence 1985a); Psephenidae (COLE), Australia (J. A. Davis 1986); Ichneumonidae (HYMN), southern continents (Gauld 1983, 1984c); Scelionidae (HYMN), Chile–New Zealand (Masner 1968); Diapriidae

(HYMN), Australia, southern continents (Naumann 1982); Formicidae (HYMN), New Caledonia–Australia–New Guinea (Ward 1985). Several contributors to Keast (1981) discuss the biogeography of Australian arthropods, although R. J. Raven's (1982) critical review is apposite. Winterbourn (1980) and Campbell (1981) review the biogeography of some aquatic insects (predominantly of running waters) belonging to several orders.

As will be seen by examination of just a few of these papers, biogeographers have many approaches, yet three partially overlapping categories can be recognised, namely: (i) ecological (physical) biogeography; (ii) dispersal biogeography, and (iii) vicariance biogeography. Dispersal and vicariance biogeography are often grouped as 'historical biogeography', but this obscures an increasing awareness that ecological biogeographic scenarios should not be made without regard to historical biotic and environmental change. Ideally biogeography requires that the phylogeny of the study group be reasonably well known (Mackerras 1970; Nelson and Platnick 1981; Cracraft 1982), although it is still prevalent for speculations to lack hypotheses of taxonomic relationship. Geographic distributional data should not be incorporated in phylogenetic hypotheses. If it were the subsequent biogeographic analysis would be compromised.

Ecological Biogeography

Plant and animal species thrive in different environments, with relatively few species widely ecologically tolerant (*eurytopic*). Ecologists are able to determine the range of optimal conditions for organisms from some populations and, by inference, for each species. Laboratory experiments in which selected environmental parameters are manipulated can show how individuals and populations respond physiologically. However, extrapolation from

laboratory results to field conditions is difficult, since among other untestable effects, competition may restrict particular taxa to a narrow band of their potential physicochemical, edaphic and other abiotic environmental tolerances. However, even in the absence of quantitative laboratory-based studies, it is clear that organisms live in preferred ranges of environmental variables, both biotic and abiotic. For example, many tenebrionid beetles occur predominantly in arid deserts, slime-mould feeding beetles in humid forests and most immature Plecoptera in cool streams. If insects are closely restricted in mutualistic, phoretic, or ecto- or endoparasitic host associations, then the distribution will reflect that of the host, though it need not fully occupy the host range. The same applies to primarily phytophagous insects whose ranges largely parallel those of the associated host plant.

Ecological biogeographers examine the broad requirements of organisms in terms of physical and climatic factors and discuss how different regions of the globe fulfil these criteria.

Given a knowledge of the factors that affect the distribution of organisms it is possible to model how these organisms will respond to such changes in the environment as temperature, rainfall or other physico-chemical characteristics of the environment (Nix 1982). In practice, modelling (using packages such as CLIMEX and BIOCLIM) begins with recording the presence of organisms at localities at which standard meteorological data are available or can be inferred. Preferably these localities include climatic extremes at which the species occurs. From these models, field occurrence can be predicted, and the actual occurrence checked against field studies. In Australia such a modelling procedure has been performed for the cattle tick *Boophilus microplus* (Sutherst and Maywald 1985). The computer-based CLIMEX model predicted the distribution of this pest species across the continent. The points in Fig. 7.3A denote localities at which *B. microplus* could survive, the larger the spot the more theoretically favourable the locality is for the survival of the species. Shading indicates the actual distribu-

tion of *B. microplus* and the correspondence between the actual and predicted distribution is very close. When climatic data from elsewhere in the world where the pest occurs (i.e. data not used to derive the original model) is put in to CLIMEX, the predicted distribution of *B. microplus* corresponds closely to the actual distribution (Fig. 7.3B). Inconsistencies occur because the distribution of an organism is not determined exclusively by climatic variables. For example, *B. microplus* is absent from parts of Africa theoretically suitable to it, due to the presence of another species of *Boophilus*, a factor not included in the mathematical model.

Although climatic modelling has yet to be fully exploited using entomological data, bioclimatic profiles derived from distribution data from specimen labels will have uses. Computer-generated, bioclimatic profiles have been used to quantify the environment occupied by Australian elapid snakes by species and by major groupings (Nix 1986).

Such procedures can be powerful analytical tools which demonstrate correlations between climate and present-day distributions for many taxa. Recognition of the geochemical and climatic constraints is necessary to understand why species introduced into areas where they previously did not occur, for example 'weeds' or biocontrol agents, flourish or fail. When applied to palaeontological data the procedures can allow estimation of past climates from faunal and floral distributions, or conversely, allow estimates of past distributions from evidence of climate.

However, these models explain only a limited number of biogeographical observations and do not address the frequent phenomenon of areas with comparable climate, soil and topography, supporting quite disparate plant and animal communities. Furthermore, the relationship between distribution patterns of higher taxa (for example, species groups, genera, families) and ecological factors is far from clear. If the predominant mode of species diversification in monophyletic lineages (clades) is via the allopatric mode (speciation in isolation) (Bush 1975)

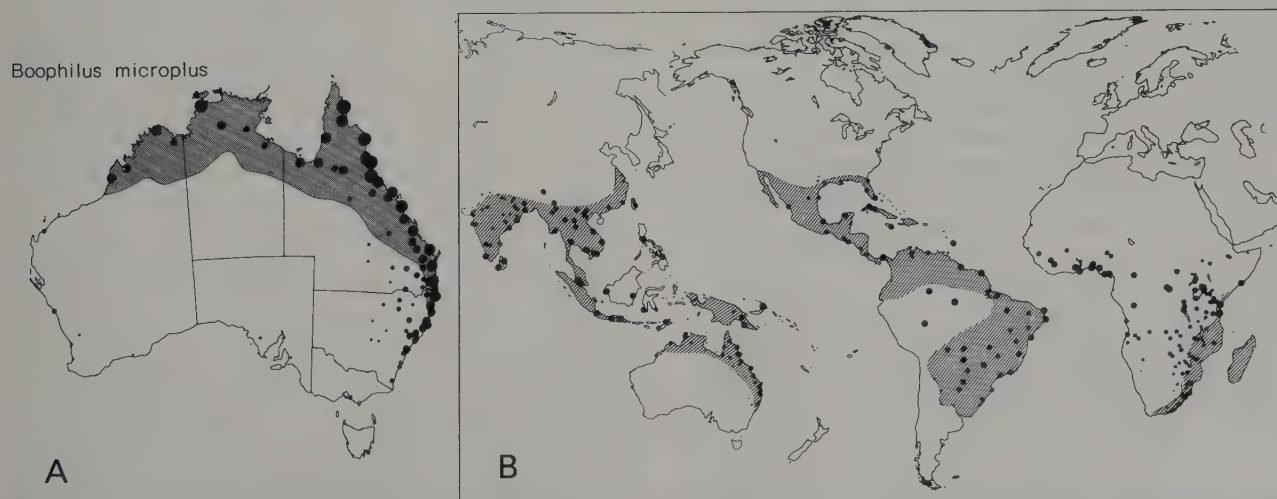


Fig. 7.3 The relationship between the actual distribution (shaded) and bioclimatically predicted favoured localities (circles) for *Boophilus microplus*: A, Australian distribution; B, global distribution. Areas of circles are proportional to theoretical favourability. [After Sutherst and Maywald 1985]

without significant ecological divergence, then we might expect that climatic models for these clades could predict the distribution. However, if the descendant taxa from speciation events diverge in their ecological requirements, or speciation is not predominantly in the allopatric mode and concurrent with ecological differentiation, we might not expect environmental parameters to correlate with distribution.

Although environmental determinants play an important role in constraining the distribution of organisms, historical factors are vital in determining the more fundamental patterns (*contra* Endler 1982).

Dispersal Biogeography

According to dispersal biogeography, disjunct distributions of related organisms arise as follows: groups originate in one place, diffuse (expand their range) until a pre-existing barrier is reached, *disperse* ('jump') across this pre-existing barrier and then differentiate in isolation (Fig. 7.7). This interpretation of biotic distributions is of long standing. It was the view promoted by Darwin in *The Origin of Species* and subsequently by Wallace (e.g. 1876), and it played an important part in the formulation of the ideas of Darwin and Wallace on species formation. Among the theoreticians of dispersal are Simpson (1940) and Mayr (1942), and the more recent proponents of this approach to biogeography include Darlington (1957, 1965), a carabidologist with a particular interest in the biogeography of the southern continents.

Central to the dispersalist approach is the view that organisms have *centres of origin* from which they migrate, disperse or diffuse to other parts of the globe. A number of criteria have been suggested for recognising a centre of origin. Such a centre would be the area: (i) most ecologically suitable for the group of organisms under consideration; or (ii) harbouring the greatest number of extant species of the group; or (iii) circumscribing the greatest morphological diversity for the group; or (iv) containing the greatest number of advanced forms with primitive forms 'pushed' to the periphery; or (v), containing the greatest number of primitive forms since advanced forms 'progressively' disperse from the origin (the reverse of (iv), and known as Hennig's progression rule). Palaeontological evidence may be sought, in the belief that the site of the oldest fossil indicates the origin of the group; however, as noted on p. 196 and in Chapter 4, p. 118, reliance upon the vagaries of the fossil record is fraught with danger. The directions of seasonal migrations have also been used to identify centres of origin with cyclical movements taken as evidence of some prior dispersal route.

Following identification of the centre(s) of origin, the next task of the dispersalist biogeographer is to trace a route for the colonisation of the remainder of the range. This involves assessment of the relative *vagility* (dispersivity or propensity and ability to disperse or diffuse from a centre of origin) of the organisms under consideration and, subsequently, detection of barriers that prevent the organisms from becoming universal.

Assessment of the propensity to disperse tends to be

somewhat subjective and arbitrary, but entomologists make some common observations. Firstly, brachypterous and apterous adult insects are presumed to have limited powers of dispersal relative to the greater mobility of winged forms. However, evidence of the ability of other life history stages (such as eggs) to survive a stressful period of dispersal can counter evidence of a sedentary adult. The occurrence of particular insects in the aerial planktonic drift is often cited as further evidence of dispersal powers. The discovery of particular insects on newly formed islands, or faunistically denuded areas, such as that following volcanic activity or marine retreat after inundation of terrestrial systems, is taken to indicate their ready dispersivity. For non-volant insects where a distribution pattern transcends physical barriers such as oceans, dispersivity is often inferred to be through contiguous land connections either extant, ancient or postulated, in combination with various *ad hoc* scenarios such as propensity to trans-oceanic rafting, elevation in cyclonic winds and in more recent times, transport, intentional or involuntary, by humans.

Once the powers of dispersal of particular taxa are known, it is necessary to consider the restrictions that completely or incompletely prevent the spreading of the taxa from their centre of origin. Commonly three kinds of filters or barriers are recognised: (i) *Corridors* or 'bottle-necks' are variably narrow constrictions of suitable habitats that may be impediments to dispersal between larger areas at each end. Ecologically similar areas so connected by corridors may have very similar biotas. In Australia, the band of savannah woodland around the base of the Gulf of Carpentaria between the sea and the arid interior, may be interpreted as a corridor connecting the savannah of the Cape York Peninsula with Arnhem Land of the Northern Territory. For example, E. G. Matthews (1972) records nearly 30 species of dung beetles shared by the savannah areas on either end of the base of the Gulf of Carpentaria. (ii) *Filter bridges* allow fewer transgressions compared with corridors, but more than the sweepstake routes (see below). Chains of oceanic or ecological islands are often cited as examples of filter bridges. The arid gap separating rainforest patches at Paluma (approximately 19°S) and Eungella Homestead (approximately 21°S) in eastern Australia, might be viewed as a filter. Ten species of dragonflies have distributions extending as far south as Paluma but no further and a different eight species occur as far north as Eungella with only three species 'spanning' the gap (Watson and Theischinger 1984a). A dispersalist interpretation is that the latter three species occur in Paluma and Eungella because they have crossed the gap, something the other northern ten and southern eight species have been unable to manage. The intermittent connections between Tasmania and south-eastern Australia and between New Guinea and the Cape York Peninsula are postulated to have acted as filters (e.g. Kikkawa *et al.* 1981). (iii) *Sweepstake routes* are major barriers, such as great expanses of ocean for terrestrial and freshwater biota, large tracts of rainforest for xeric forms or extensive tropical regions for cold-adapted stenothermic organisms. Generally it is held to be a mat-

ter of chance which organisms will survive a sweepstakes route and successfully colonise the new area. Dispersal via sweepstakes routes is commonly invoked to explain the depauperate, unbalanced mixture of taxa found on remote islands. Thus, Norfolk I., lying isolated in the south-western Pacific Ocean some 700 km from Australia, New Caledonia and New Zealand, has a tiny fauna of sphecids wasps of six non-endemic species in two genera. This in no way reflects the sphecids faunas of the areas from which Norfolk Island species are presumed to have originated. In Australia, for example, there are over 750 species of sphecids in about 50 genera, in New Zealand 16 species in eight genera. In contrast to Norfolk I., Hawaii is a spectacular example of a chain of islands (some now submerged) with a diverse insect fauna apparently derived from a handful of transoceanic colonists (Zimmerman 1948).

A classic dispersalist analysis of biogeography is Darlington's (1965) interpretation of the history of several tribes of carabid beetles which have extant, temperate-zone distributions on either side of the Tropics (i.e. *amphitropical* distributions). Darlington believed that his tribes originated on the large land masses of the Northern Hemisphere (particularly the more tropical portions of these land masses) and subsequently dispersed southwards by separate routes into South America and Australia (Fig. 7.4A) and from Australia some then spread to New Zealand. The more tropical forms became extinct, leaving an amphitropical distribution pattern with representatives in the Northern Hemisphere and on three of the Southern Hemisphere land masses (Fig. 7.4B). Further

extinctions in both hemispheres then account for distribution patterns such as depicted in Figs 7.4C and D.

Dispersal has always been central to explanations of island biotas. Fig. 7.5 shows the distributions of several species of ponerine ants in Indonesia and the south-western Pacific. Those species depicted in Fig. 7.5A are regarded by Wilson (1959) as Asian species apparently expanding their ranges along the Indonesian-Melanesian island arc. The distribution patterns show the ponerine ant fauna becoming more attenuate as the distance from Asia increases and also suggest successive waves of colonising ants spreading east. Some other ponerine ants have distribution patterns as depicted in Fig. 7.5B. These are regarded as local endemics or groups of endemics derived from one or other of the eastward-spreading waves of ponerines. Similar patterns, for example in beetles (Gressitt 1956, 1961) and butterflies (J. D. Holloway 1973), have encouraged many dispersalist biogeographers of the south-western Pacific region to visualise a cycle of eastward expansion followed by local speciation or radiation.

The theory of island biogeography of MacArthur and Wilson (1967) is a mathematical elaboration of dispersal biogeography. Among other things, this theory postulates a relationship between species and area, such that larger islands support a more diverse biota, through greater habitat diversity, than do smaller ones. MacArthur and Wilson (1967) and others visualise an island biota in or approaching a dynamic equilibrium. At equilibrium, immigration and extinction rates are equal, so that the total number of species on an island is constant. However, the actual composition of the biota changes with time, as species interact and geological and/or climatic changes occur. Thus observations by Wilson (1985b) of the alteration in the generic composition but stability in total number of genera of Dominican (West Indies) ants since the late Oligocene/Miocene [about 20 mybp (million years before present)] are taken to support the predictions of the MacArthur and Wilson theory. 'Genera' are constructs and species information would have provided a better test. Case and Cody (1987) caution against the uncritical acceptance of some or all of the predictions of the theory, based on the results of their studies of islands in the Sea of Cortez.

Theories concerning explanations of island biotas, whether dispersalist or vicariant (see below) have wide application in biogeography. There is little difference between a remote coral atoll, an isolated patch of rain-forest, a lake and a high mountain peak—all can be envisaged as 'islands' isolated by surrounding unsuitable habitats.

Criticisms of dispersalist biogeography. Dispersalist explanations of biotic relationships between disjunct areas originated when the fixity of present land masses was unquestioned. If land masses did not move then disjunctions must have arisen by movement of the biota and mechanisms needed to be postulated, as outlined above. All observed distributions became explicable by one or a combination of these above scenarios of faunal relocation, with differential extinctions explaining absences.

Although dispersal scenarios are made for groups with

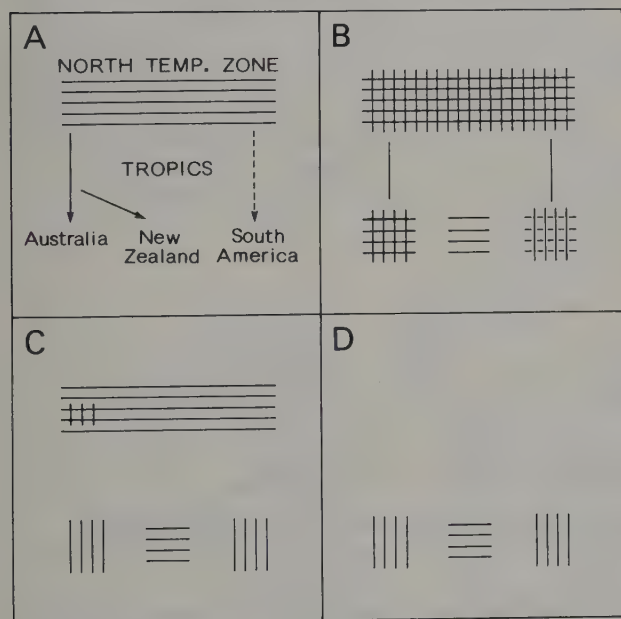


Fig. 7.4 A dispersalist interpretation of disjunct distribution patterns of austral carabid beetles: A, An initial, northern stock disperses south to South America and Australia with further dispersal to New Zealand; B, A second stock disperses from north to south, but not to New Zealand; C, The first stock becomes extinct in Australia and South America and much of the northern zone, leaving relict distribution in the north and in New Zealand; D, Both stocks disappear in the north leaving relicts in the austral regions. [After Darlington 1965]

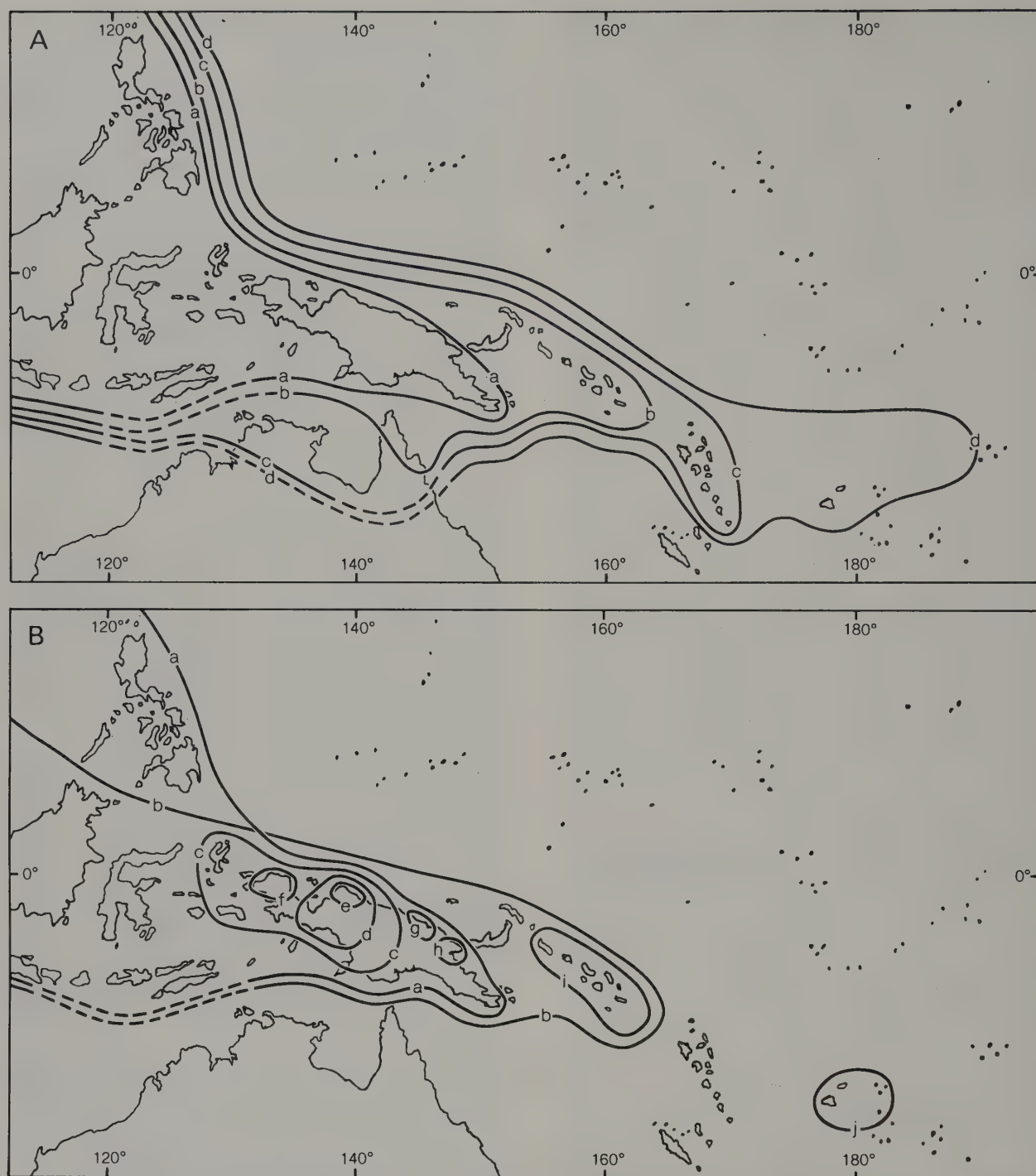


Fig. 7.5 Distributions of ponerine ants: A, postulated to be the result of Asian species spreading eastwards; B, indicating groups of local endemics.

[After Wilson 1959]

understood phylogenies, there have been few attempts to relate phylogeny to distribution—each species has been treated as an individual case, and, generally, congruence between distribution and phylogenetic relationship has not been sought. Congruence of repeated patterns might imply similar histories of dispersal for the organisms investigated and repeated *ad hoc* explanations can account for any distribution pattern.

The dispersalist view postulates speciation occurs after the crossing of barriers. Some writers have questioned whether a barrier that allows a founder population to cross in one direction can be a total barrier to subsequent exchanges that would prevent allopatric speciation.

A most cogent criticism concerning 'jump' dispersal across a barrier followed by establishment is that this implies dispersal into some kind of ecological vacuum.

Here biogeography must take more cognisance of ecological theory (Myers and Giller 1988). There is no doubt that dispersal occurs and we have clear, recent evidence that newly formed or denuded areas such as post-volcanic Mount St Helens (USA) or the island of Krakatoa (Indonesia) (see papers in *Phil. Trans. R. Soc. Lond.* **322**: 273–522, especially Thornton and New 1988) are rapidly colonised. Further examples on a rather longer geological time scale are the acquisition of post-glacial floras and faunas by the British Isles and vast areas of the cool temperate zones of the Northern Hemisphere and New Zealand by post-Pleistocene colonisation from non-glaciated areas. None the less, for an increasing number of biogeographers, dispersal alone is an inadequate mechanism to account for the regular structuring of the distribution patterns observed.

Vicariance Biogeography

Evidence of disjunct distributions of taxa identical to that which led dispersalists to argue for mobility of the biota between static continents, can be used to adduce mobile land masses and static biotas. Although the ideas do not originate with Leon Croizat as he himself acknowledges (1958: Introduction), Croizat is now credited with promulgating the view that present biotic distributions represent fixed, ancient patterns that have been disrupted, ‘vicariated’ in the past by geology and climate. Croizat’s method involved compendious documentation of the distributions of many organisms, mapping these distributions and connecting distributions of related taxa by lines (*tracks*). He found that there were repeated occurrences of relatively few lines (*generalised tracks*) (Fig. 7.6) across the globe, even when masses of unrelated taxa were considered, but that these did not bear any direct relationship to modern geography. Thus in the Southern Hemisphere generalised tracks cross the oceans, linking distant land masses, and in the Northern Hemisphere traverse mountain ranges. Croizat (1964) argued that the congruence (or regularity) of so many distributions to form generalised

tracks could not be explained by dispersal. Instead, they were evidence for the appearance of impassable barriers dividing many taxa, thus producing congruent patterns of speciation, whose geographic relationships were identical. In the terminology of historical biogeography, widespread ancestral species are divided into *vicariant* populations (incipient species) by a *vicariance* event, which may arise through geological or climatological occurrences such as sea level alteration, ocean formation, orogeny, aridity or glaciation. In dispersal biogeography the barrier predates the disjunction, but in vicariance biogeography the barrier *causes* the disjunction (Fig. 7.7).

In developing his methods, referred to as *panbiogeography*, Croizat did not make explicit his means of assessing taxonomic relationship (McDowall 1978; Ball 1981) and he and his followers (*‘panbiogeographers’*) rely on some intuitive estimate of overall similarity rather than cladistic phylogenetic analysis (e.g. Croizat 1982; Craw 1983, 1988). When Croizat’s studies were incorporated with a strictly cladistic phylogenetic method (Croizat *et al.* 1974) (and thus became exposed to a wider audience) Croizat’s negative views on the centrality of phylogenetics were not accurately represented. None the less, the fusion of cladistic phylogenetics and vicariance biogeography became the framework for the *cladistic vicariance biogeography* espoused by many subsequent historical biogeographers.

Hennig’s explicit method for phylogenetic reconstruction (Chapter 4) provided a framework within which biogeographic patterns could be examined. Examples of the use of phylogenetics in biogeography were given by Hennig himself (1960), Illies (1965) and Brundin (1966). Thus, when Croizat’s views had been combined with cladistics, many biologists, particularly European entomologists, were receptive. However, many retained dispersalist ideas of centres of origin and a belief in Hennig’s ‘progression rule’ (plesiomorphy in a centre of origin, with increasing apomorphy peripherally) rather than the exclusively vicariant paradigm espoused by

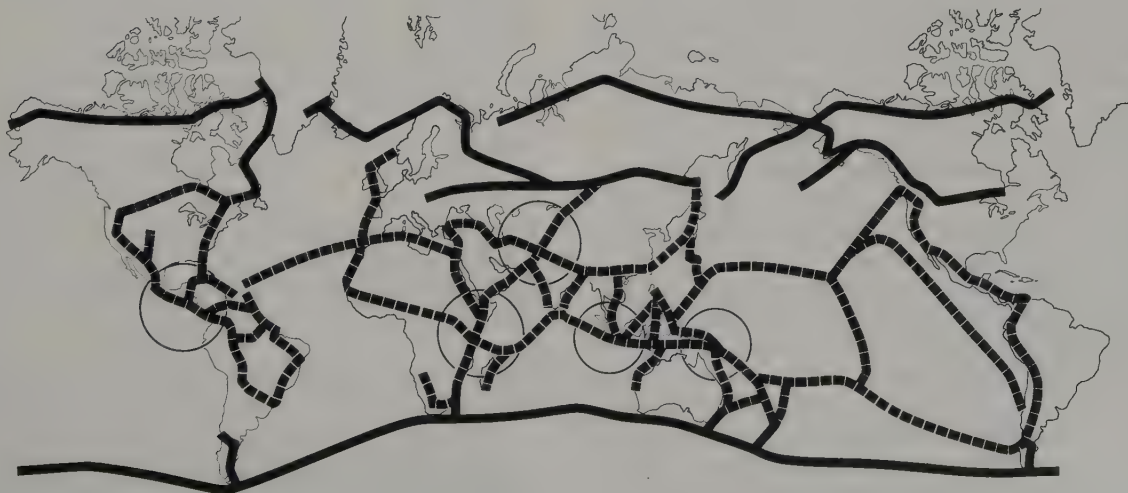


Fig. 7.6 Summary of generalised tracks of the world (after Croizat 1958). Solid tracks are boreal and austral.

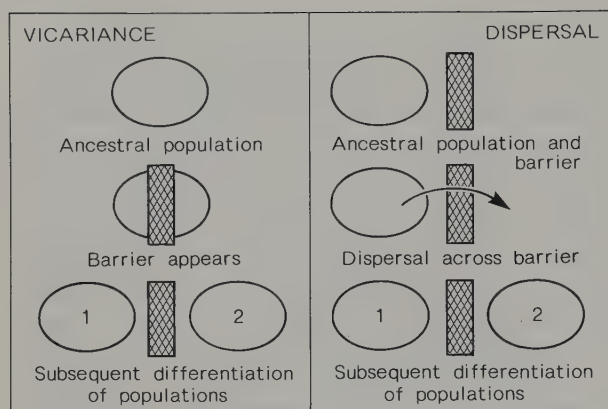


Fig. 7.7 The significance of barriers in vicariance and dispersalist explanations of disjunction. [After Nelson and Platnick 1984]

Croizat, Nelson (1974, 1978b), Nelson and Platnick (1981) and Humphries and Parenti (1986).

The two vicariance methods, cladistic and panbiogeographic, have moved in separate directions, with the cladists stressing the primacy of phylogeny and the panbiogeographers emphasising distribution pattern and proximity of related taxa. Panbiogeographic studies since Croizat stem predominantly from a New Zealand school, and include those of Craw (1985, 1988 and references therein), Craw and Page (1988) and Gibbs (1983). Recent developments in panbiogeography include attempts to quantify the length of tracks using graph theory (Page 1987, 1988)

The reason for the interest in vicariance in biogeography compared with dispersal scenarios was the increasing acceptance that continents were not fixed, but were mobile, a view stated by Wegener (1915) in his theory of *continental drift* (see plate tectonics, p. 190). If land masses moved then disjunct distributions could be explained by ancient proximity, since disrupted. Croizat's generalised tracks linked faunas that were originally contiguous—instead of mobile faunas dispersing on a fixed geography, immobile faunas were dispersed on moving plates of land. Thus, Hooker's (1853) observation of the similarity of the southern plant faunas now had a new explanation (Brundin 1966, 1988) and most dispersalist, faunal interpretations of Darwin and Wallace and many successors who believed in a stable geography, could be refuted. Before proceeding to an outline of the present views on plate movements and historic climate, some examples of the application of the techniques of vicariance biogeography are appropriate.

Fig. 7.8A depicts a cladogram for a group of mayflies (EPHM) (after Edmunds 1981). The cladogram includes four monophyletic lineages each of which comprises three genera and each genus is endemic to either New Zealand, Australia or South America. *Nesameletus*, *Oniscigaster*, *Ameletopsis* and *Coloburiscus* are restricted to New Zealand, *Ameletoides*, *Tasmanophlebia*, *Mirawara* and *Coloburiscoides* to Australia, and *Metamonius*, *Siphonella*, *Chaquihua* and *Murphyella* to 'Magellania'

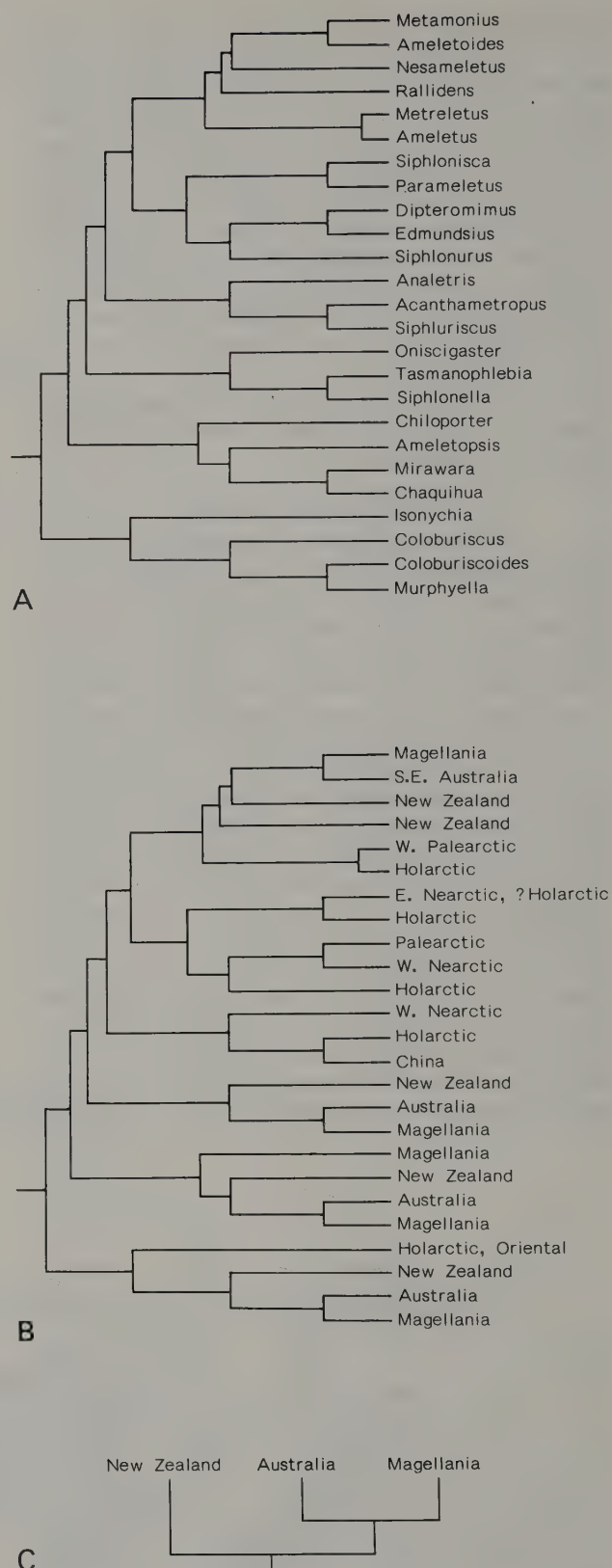


Fig. 7.8 A, cladogram showing relationships among Siphonuridae and some Oligoneuriidae (EPHM) (after Edmunds 1981); B, area cladogram derived from A; C, area relationships between Magellania, New Zealand and Australia as evidenced by four monophyletic sub-groups (see text).

(southern South America). When taxon names in a cladogram are replaced by their respective areas of endemism, the result, called an *area cladogram*, shows the historical relationship of the areas as evidenced by these mayflies (Fig. 7.8B). In this example, the area cladograms derived from each of the four monophyletic mayfly sub-units (Fig. 7.8C) are identical (*geographically congruent*) and imply that for these mayflies the Australian and South American land masses share a more recent history than either do with New Zealand. Comparison of the area cladogram (Fig. 7.8C) with theories of earth history reveal a possible explanation of the processes that might have determined the observed pattern. Thus, until the late Cretaceous, Australia, South America and New Zealand (in part or as a whole) were connected in a great Southern Hemisphere land mass *Gondwana* (see p. 191) with Antarctica the centrepiece. When fragmentation took place, land connections between Australia, New Zealand and South America were not severed simultaneously: New Zealand (at least in part) became isolated first while Australia and South America retained land links through the Antarctic until later. Thus the first vicariance event was the splitting of the original widespread taxon into a New Zealand isolate and an isolate on Australia–South America and in a second vicariance event, the Australian–South American isolate was itself divided.

A cladogram depicting the relationships among the 16 species of a monophyletic group of non-biting midges (DIPT: Chironomidae) of the genus *Parochlus* is shown in Fig. 7.9A, from data of Brundin (1966). The species are distributed over the same land masses as the mayfly genera in the preceding example, except that one species (*P. kiefferi*) occurs in North America. Fig. 7.9B is the reduced area cladogram (with redundant distributions removed) derived from 7.9A. It depicts several New Zealand–South America vicariance events and one Australia–South America vicariance event occurring after an event involving Australia–South America–New Zealand. Accumulating evidence on the probable polyphyletic (polyterratic, composite) origin of New Zealand (e.g. Craw 1988) suggests these patterns might profitably be re-examined.

In the same way that the distribution of a single taxon can be interpreted by a dispersal scenario, a single cladistic analysis transformed into an area cladogram can always be interpreted. Explanatory power increases with addition of many geographically congruent area cladograms. As with Croizat's generalised tracks, the more similarity in pattern that is discovered, the stronger is the evidence that disjunct distributions were determined rather than arose through the supposedly stochastic mechanism of jump dispersal. Thus vicariance biogeographers are concerned with detecting patterns for as many groups as possible and examining the area cladograms for congruence.

Difficulties with Vicariance Biogeography. Area cladograms are only as good as the phylogenies from which they are derived. Phylogenies can be derived in different ways. They can be based on sound data and hypotheses or on less certain grounds. Ideally, the vicariance biogeographer would have intimate knowledge of

the phylogenies of all groups of organisms, and thus be able to assess the relative merits of phylogenies. In practice, this is often not possible and phylogenies are taken on face value. Some of the problems of incongruence between area cladograms demonstrated by Noonan (1988) may stem from the different approaches to deriving phylogenies. Furthermore, few cladograms have been tested for robustness and it could well be the case that an apparently incongruent area cladogram is no more robust than a fully congruent one.

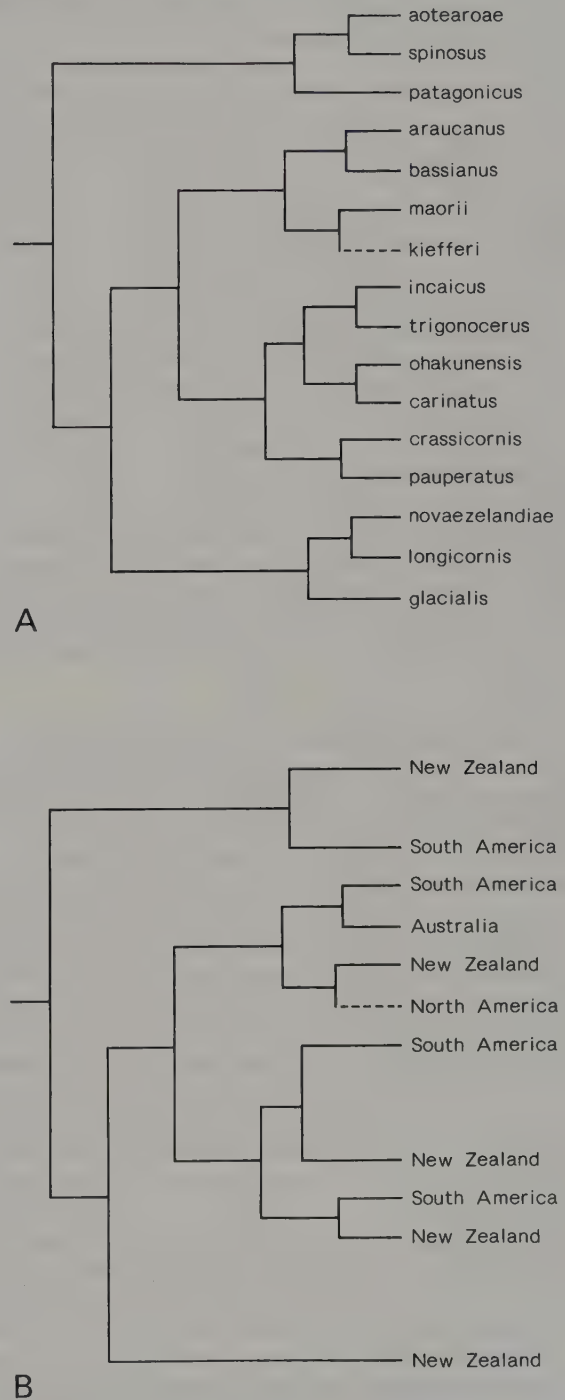


Fig. 7.9 A, phylogeny of the *Parochlus araucanus* group (DIPT: Chironomidae) (after Brundin 1966); B, reduced area cladogram from A.

Further difficulties arise when well substantiated area cladograms remain incongruent. This can arise due to the effects of redundant data, extinction, the existence of unique taxa (or areas) and/or the occurrence of widespread taxa that overlap endemic areas defined by others. Methods of addressing these difficulties parallel some of those available for reconciling character conflict in cladistic analyses (Chapter 4), and include component analysis and several parsimony methods, explained in detail by, among others, Nelson and Platnick (1981), Humphries and Parenti (1986), Zandee and Roos (1986), Humphries *et al.* (1988) and Wiley (1988). One of the common findings when variably incongruent area cladograms are compared is that the resulting combined area cladogram may be trite, doing no more than documenting the geophysicists' view of the breakup of the main plates of Gondwana. Fine level area cladograms, for example concerning the biota of parts (terrane) of Gondwanan South-East Asia, are scarce (e.g. Schuh and Stonedahl 1986).

Vicariance paradigms assume that a single history of the earth is reflected in the patterns of evolutionary relationships and distribution through the world. Dispersalists argue that congruences of dispersal could explain similar patterns, although the mechanism that might produce such concerted movements through history is not evident. Vicariance biogeographers do not ignore dispersal, but reject its primacy. Dispersal that produces incongruence in area cladograms is the equivalent of homoplasious character states in a phylogenetic analysis of characters. None the less, dispersal is recognised, particularly when there is evidence of the historical removal of barriers, and is the means by which ancestral distributions arose prior to vicariance events.

Plate Tectonics and Palaeogeography

The propensity of biologists such as Tillyard and Croizat to unite continents or raise and sink land bridges at will was viewed coldly by geologists (Mackerras 1970). Although there were early catastrophist theorists that advocated mobile continents (see review by Bishop 1981) and Taylor (1910) invoked continental displacement in relation to Tertiary orogeny, Alfred Wegener was the first to assemble evidence that supported a theory of drifting continents (the English edition of Wegener, 1915 appeared in 1924). However, although the ideas stimulated much controversy, the traditional views of stasis prevailed because geophysicists were unable to envisage a viable mechanism in view of the rigidity of the crust. No known mechanism existed for moving continents of harder sial floating in isostatic balance on more dense, more viscous sima.

Many Northern Hemisphere zoogeographers were pre-occupied with the analysis of Tertiary radiations, and did not question the static view of world geography. Only a few biologists, predominantly in the Southern Hemisphere, found it impossible to account for the abundance of disjunct relationships among the southern continental biotas as marginal relicts derived from the north, or evolutionary convergences, or the results of trans-oceanic

dispersal across the oceans separating the southern lands. Even the demonstration that Antarctica had supported a substantial palaeoflora failed to explain how Australia had acquired ancestral stocks with southern, especially South American, affinities. With Wegener's hypothesis, biologists such as Harrison (1928) rapidly recognised that many major problems of southern zoogeography had become explicable, and that early biological proponents of a united, southern continent, such as Hooker (1853) were indeed correct. None the less, it took over fifty years before the geophysicists were prepared to adopt the hypothesis so readily accepted by their fellow biological scientists.

By the mid 1960s, evidence of mid-oceanic ridges, magnetic anomalies on the sea floor, and palaeomagnetism, had suggested a geophysical mechanism (sea-floor spreading) for lateral displacement of continental plates, and encouraged palaeogeographers to accept continental drift. The drifting apart of the southern continents from a previous juxtaposition provides the most coherent explanation for closely related biotic communities, surviving today as geographically dispersed assemblages. Many of the ideas concerning the origins of the Australian flora and fauna, now supported by evidence from palaeoclimatic and palaeontological studies, are consistent with the data derived from purely geophysical sources, concerning the palaeogeographic history of the continent.

Plate Tectonics and Expanding Earth

The theory of *plate tectonics* incorporates the seafloor spreading mechanism for continental drift to explain global geological and geophysical patterns such as the observation that earthquakes occur in a linear pattern over the earth's surface. The earthquake lines enclose large, aseismic regions where earthquakes are rare. The relatively aseismic areas are the so-called 'plates' and may include both oceanic and continental crust. The plates, which make up the surface of the globe, act as rigid bodies, and their relative motion causes deformation along their junctions, releasing energy which is expressed by earthquake activity.

Plate boundaries may be divergent or convergent. In the first, two plates move apart, displaced by the accumulation from beneath of new crustal material along their adjacent margins. The new crust wells up as volcanic lava, to form a ridge between the plate margins, and the spread of young crustal material outwards from this ridge drives the system. These *spreading ridges* are situated predominantly in the great ocean basins. The modern Australian plate has one spreading ridge extending west-east between the continent and Antarctica, and another (inactive since the Eocene) extending from north-west of Timor to beyond north-eastern New Guinea (Audley-Charles 1987, Figs 2.1–2.7).

Convergent, plate boundary lithosphere is lost as two plates collide and the crust of one plate is forced back (subducted) into the earth's mantle under the edge of the other. Deep oceanic trenches and volcanic island arcs form where oceanic crust lies on both sides of a conver-

gent boundary. Where continental crust is involved folded mountain systems are formed. The mountains of New Guinea are an example of land being forced upwards at a collision front. As the Australian plate approached and made contact with the islands of the Banda Arc, complex subduction trenches formed throughout South-East Asia. These trenches were orientated predominantly in a north-west to south-easterly direction (Audley-Charles 1987, Figs 2.6–2.9).

A third type of plate boundary results when plates slide past each other to form transform faults. These may occupy large sections of a plate margin. An example of a transfer fault is the seismically active San Andreas Fault in California. This fault forms the north-eastern margin of the Pacific plate. A postulated, north-south fault at 'Ninety East' (longitude 90°E) in the Indian Ocean is believed to be the dominant transform fault where the eastern margin of the Indian plate moved northwards relative to the Australian plate (Audley-Charles 1987, Figs 2.6–2.8).

Palaeocontinental reconstruction, which seeks to trace the past movements of continents towards their present positions, depends upon evidence from various sources. These include the matching of opposite, continental margins and their geological formations and strata (the fundamental evidence invoked by Wegener), the analysis of directional palaeomagnetism stored in rocks and strata, particularly the linear pattern of magnetic reversals which is the prime evidence for sea-floor spreading, and the physical measurement of rates of continental motion.

Although the central ideas and mechanisms of plate tectonics are now widely accepted, there are competing hypotheses concerning some features. When reconstructions of continental displacements are made on a globe of current dimensions, the continental margins are a close but imprecise fit, even if the appropriate corrections for projections of a globe on to a flat plane are made (Owen 1981). A more impressive fit results when the continents are reassembled on a globe of reduced dimensions, in keeping with the *expanding earth* hypothesis of Carey (1975, 1976). Observations that support this hypothesis include the lack of adequately ancient oceanic crust and/or the existence of appropriately located subduction zones that must have existed without earth expansion. Continental reconstructions made on a present dimension globe may be contrasted by comparing reconstructions on globes of constant and postulated smaller earlier dimensions (Owen 1981) and Howarth (1981). As with the long rejection of continental drift by geophysicists, the expanding earth hypothesis has not been widely accepted because of several geophysical objections, for example the implications of variations in the value of the Universal gravitational constant. None the less, the concept of an expanding earth carries serious implications for biogeographers, some of which are considered below.

Australian Continental Palaeogeography

As described above, some biologists recognised southern continental, biotic connections that encouraged their early

acceptance of Wegener's hypothesis of continental mobility. In this biologists long predated the geophysicists in accepting such ideas. In contrast, those who fitted biogeographic patterns to a prevailing static version of earth history requiring long-distance dispersal or hypothetical land-bridges to transport the fauna, are now seen to have been misled by the contemporary geophysical dogma. The warnings made by Ball (1976) and Archer (1984) to biogeographers and palaeontologists to avoid rationalising their data to conform to current geological opinion are well taken. None the less, testing faunal distribution patterns for congruence against theories of regional earth history can provide valuable substantiation for biogeographic theories. Thus a short section on contemporary ideas concerning Australia's geological history is apposite.

Before the mid Jurassic (about 188–160 mybp (million years before present)) the present continental areas were aggregated in a single land mass named Pangaea. Australia was contiguous with the Antarctic to the south and India to the west. The future New Zealand and New Caledonia probably were to the south-east coast of Australia or against the eastern margin of East Antarctica. The future New Guinea was on the same plate as Australia, lying in the same relative position on the northern margin as it does today. Models differ as to the proximity of Asia and fragments that were to become South-East Asia (see below).

During the later Jurassic, Pangaea became progressively divided by the expanding Tethys Ocean, which separated the former supercontinent into northern ('Laurasia') and southern ('Gondwana') land masses (Fig. 7.10). Laurasia subsequently fragmented to form North America, Europe and much of greater Asia, while Gondwanan fragmentation resulted in greater India, Madagascar, Africa, New Zealand, South America, Australia and many smaller fragments (*terrane*s) such as New Caledonia, Burma/Malaysia, Borneo and some other islands of the Sunda Arc (Audley-Charles 1987).

The fragmentation of Gondwana resulted in a sequential sampling of different parts of an ancestral Gondwanan biota. Although Gondwana was a single land-mass it is unlikely that its biota was homogeneously distributed. Taxonomic diversification must have occurred on Gondwana before its break-up, but we have little idea of the factors or vicariance events that influenced the early diversification process. The postulated sequence of Gondwanan break-up and the approximate dating is as follows:

If an earth of constant dimensions is assumed, then Jurassic separation of Gondwana from Laurasia involved the development of a deep ocean, the Tethys, that was broadest at the eastern end (north and west of Australia) and narrowest at the western end, where the Mediterranean is a relict. Exponents of an expanding earth find no requirement for (and little evidence of) a broad, deep Tethys Ocean, envisaging only a narrower shallow epicontinental sea (cf. Figs 12.3 and 12.4 in Owen 1981). These different interpretations have profound biogeographical implications, but have been little tested.

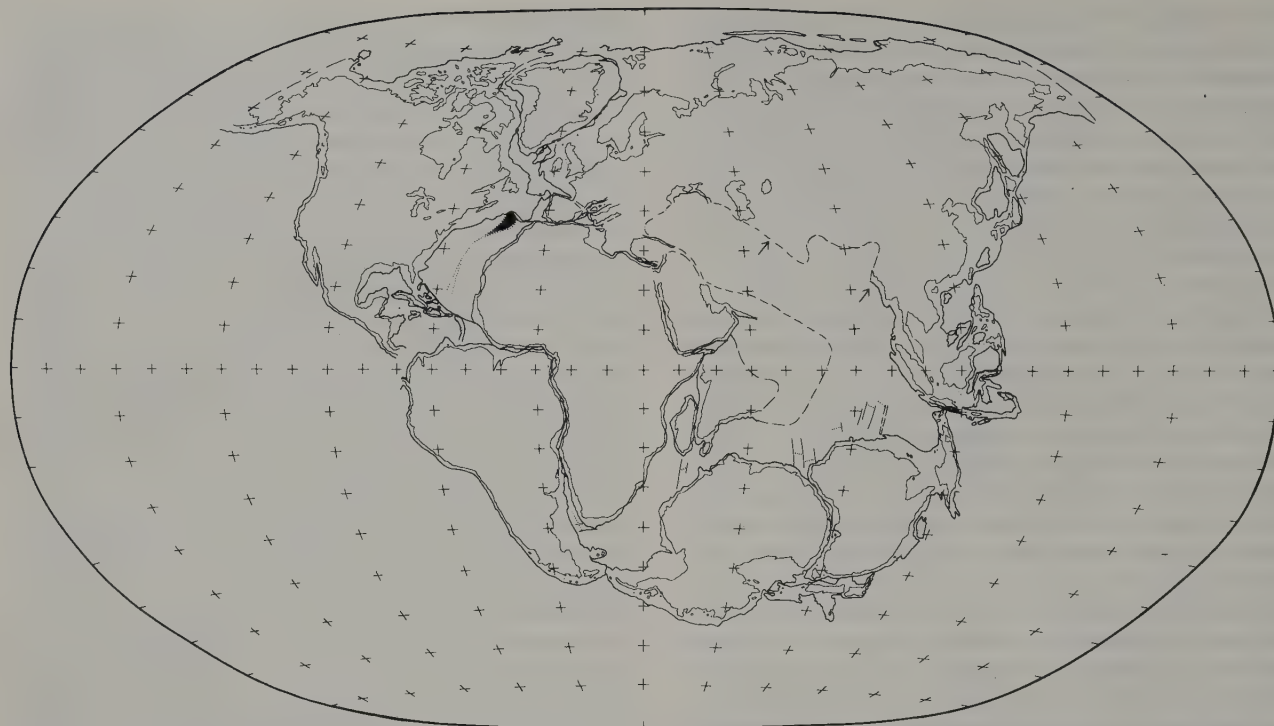


Fig. 7.10 A reconstruction of Gondwana (and Laurasia) in the Lower Cretaceous (120 mybp) on an earth of constant dimensions.

[After Owen 1981]

Following movement southwards in the Jurassic, Antarctica became central to Gondwana, and, although some rotation has taken place, its position has been relatively stable since the mid-lower Cretaceous (c. 120 mybp). Thus it is convenient to relate the continued break-up of Gondwana to Antarctica. Within Gondwana, fragmentation began in the upper Jurassic (c. 157 mybp) when a deep oceanic trench formed between west Gondwana (South America + Africa) and east Gondwana (Madagascar + India + Australia + New Zealand + Antarctica), and a seaway started to open between Australia + contiguous Antarctica and south-eastern Africa, forming a proto-Indian Ocean. The northward movement of India, towards Laurasian Asia commenced in the early Cretaceous (about 133 mybp), with separation from Madagascar by the late Cretaceous (84 mybp). Rift faulting between southern Africa and Antarctica that started in the Upper Jurassic (c. 155 mybp) continued as Africa moved northwards and rotated anti-clockwise, leading to an apparently southerly movement of Madagascar as it separated from India.

New Zealand, or at least part of its modern land mass, was probably the next major fragment to depart from the remnants of Gondwana. It appears to have been located on the eastern margin of Gondwana, perhaps associated with antarctic Marie Byrd Land (Zinsmeister 1987). Suggestions that New Zealand separated from Gondwana about 80 mybp need substantiation, as do ideas of a multiple origin for the islands (Craw 1988). The islands of New Caledonia, Lord Howe and perhaps also Norfolk, are of continental origin and probably have retained relative proximity to New Zealand (though varying in

distance from Australia) since their departure from Gondwana. New Caledonia is continental, lying at the northern end of a submerged, shallow ridge that connects it with New Zealand (J. D. Holloway 1979). Lord Howe lies towards the northern end of the predominantly submerged Lord Howe Rise, upon which Norfolk Island also lies, both being continental crust that also originates close to New Zealand (Hutton 1986).

The remaining Gondwanan land mass, which comprised Antarctica, Australia and South America remained more or less integral for a further period and the later separation of South America from the eastern Antarctic peninsula is more complex. A number of crustal blocks have been recognised in a composite arc through peninsular Antarctica and southernmost South America. Throughout the period the western edge of South America and eastern Antarctica was a subduction zone of the south-eastern Pacific and a great deal of tectonic uplift took place throughout the Cretaceous. The Antarctic itself may have been divided by a Cretaceous seaway (Zinsmeister 1987). The geological evidence concerning mobility of faunas between South America and Australia through Antarctica and the effectiveness of barriers within the area is unclear.

At the opposite end of the remnant Gondwana, the initiation of a deep, west-to-east directed, channel between western Australia and eastern Antarctica had commenced in the late Jurassic (160–140 mybp). By the Upper Cretaceous (80 mybp) a deep sea trough extended to the (modern) mid-Victorian south coast of Australia, though its width may have been narrow (Zinsmeister 1987). Completion of the isolation of Australia through the

development of a continuous seaway connecting the Indian and Pacific Oceans apparently did not occur until the early Tertiary (c. 60 mybp) and a remnant South Tasman Rise, a land bridge linking south-eastern Australia with Antarctica, does not appear to have been lost finally until about 38 mybp (Zinsmeister 1987).

Following its separation from proto-Antarctica the Australian plate moved northwards during the mid-Tertiary, across about 30° of latitude in about 20 million years. Although the conventional view has been of an isolated Australian plate with thousands of kilometres of open ocean to the north, this is increasingly questioned. Audley-Charles (1987) summarises the view that South Tibet, Burma, the Thai-Malay Peninsula and Sumatra (called the Sunda Arc or Sundaland) originated in eastern Gondwana attached to northern Australia + New Guinea, a hypothesis first suggested by Ridd (1971). Although the timing is uncertain, these Gondwanan, Asian terranes probably rifted away in the Jurassic, if not earlier. Whatever the timing, these terranes were present to the north and north-west of the Australian plate, between it and Laurasian Asia, during the Cretaceous and early Tertiary. The islands of the Outer Banda Arc (including Timor, Seram and eastern Sulawesi) undoubtedly are part of the Australian plate and show no signs of ever having rifted from the Australian continent. Thus, throughout the Cretaceous and early Tertiary there were continental fragment(s) of Gondwanan origin lying between Australia and mainland Asia.

As the continent approached South-East Asia in the mid-Miocene (about 15 mybp), the Australian Plate came into contact with the Sunda Island Arc, which extended south-eastwards from Asia. At this time the Sunda Arc was reorientating anticlockwise to provide a series of island 'stepping stones' between the approaching Australian plate and mainland Asia. The mid-Miocene impact of the Australian plate was associated with uplift of the fold mountains which now constitute the axial cordillera of New Guinea, and volcanic activity occurred causing formation of new land areas between New Guinea and South-East Asia. Previously this collision has been given great importance as the time at which biotic elements from the north ('Oriental', 'Papuan') 'intruded' into Australia and reciprocal exchanges took place with Asia.

The geological complexity and probable, multiple tectonic origin of the islands to the north-west of the Australian plate is an obvious reason for the difficulty biogeographers have faced in drawing lines to separate the Oriental and Australian biogeographic regions (e.g. Simpson 1977; George 1981). The biogeographic consequences of a reassessment of activities at the northern margin of the Australian plate for botanical, particularly angiosperm, biogeography are addressed by Truswell *et al.* (1987) and Audley-Charles (1987). Perhaps the most important implications are that the 'northern' element in the Australian biota might not be entirely Laurasian, but could include representatives of an earlier Gondwanan fauna with a separate evolutionary history from the more southern 'Antarctic' ancestors. The significance of disper-

sal into Australia after the Miocene contact, previously postulated to explain the presence of these 'northern' elements, is questioned by Truswell *et al.* (1987) on the basis of lack of palynological (pollen) evidence for any mass invasion of 'intrusive' taxa at this time. The reassessment of the origins of Australia's rainforest as autochthonous rather than a dispersal-derived and impoverished version of that of South-East Asia (Webb *et al.* 1986) carries a salutary message to entomological and other biogeographers concerning untestable, dispersal scenarios.

Palaeoenvironments of Australia

When the Australian plate left Gondwana it was populated with a distinctive sample of the biota, presumed to have included elements endemic to (i) Gondwana relative to Laurasia, (ii) eastern Gondwana relative to western Gondwana and (iii) the Australian plate (or parts thereof) relative to proximate areas. Although the concept of the plate being an isolated 'Noah's ark' during the Tertiary is now challenged (see above), there is little doubt that the period saw a radiation of the biota with a unique history. It is pertinent to examine palaeoenvironmental change in relation to putative vicariance events that give rise to the complexity of the present day biota. The evidence for environmental change comes from sources as diverse as fossil animal and plant (including spore and pollen) assemblages, geological records of sedimentation and weathering, and isotope ratios giving past sea temperatures. Data from these sources are often ambiguous and environmental reconstruction based on them is controversial. For example, the recent Quaternary (1.6 mybp to the present) climatic changes are of such complexity and associated with such dramatic alterations in ranges and extinctions (Gentry and Sutcliffe 1981; De Deckker 1986) that current interpretations of events in earlier geological time might be seen as facile and speculative at best.

Much of the data from which climatic reconstructions are derived stem from palynology, using pollens to identify past plant communities. The extrapolation from these communities to earlier climates depends upon untested assumptions of uniformitarianism—that present ecologies are identical to those of the past. Australian palaeoenvironments are better known than the insects that inhabited them, although Kukalová-Peck (Chapter 6) lists the fossil insects recorded from Australia through geological time and the role of fossils in biogeographic analysis is discussed below. The recording of the predominantly plant-based palaeoecosystems below is of relevance, however. Many insects are intimately associated with plants and the historic radiation of many groups is coincident (Schlinger 1974; Schuh and Stonedahl 1986) and biogeographic coevolution of plants and insects may occur (Humphries *et al.* 1986).

Reconstructions of the changing Australian environment are in a state of flux. The précis below is derived largely from Barlow (1981), J. M. B. Smith (1982), P. H. Raven (1983), Kershaw (1988) and various chapters in Keast (1981) and Barker and Greenslade (1982).

Alpine glaciation in the late Carboniferous intensified into the early Permian when ice sheets centred on an

Antarctic South Pole covered much of Gondwanan Pangaea, including much of western, north-central and southern Australia (Audley-Charles 1987, Fig. 2.2). In the warming, later Permian climate, Australia and other parts of Gondwana supported a flora dominated by a now extinct group of gymnosperms, the glossopterids. These shrub- and tree-like plants occupied extensive, cool temperate swamps. Tree ferns were abundant and conifers occurred in drier areas. Many plants were deciduous and dormant during the severe, cold winters.

In the Triassic, pteridosperms, ferns, ginkgos, early cycads and podocarp conifers grew in an at first cool temperate but increasingly warm and dry environment. Increasingly, molecular clock-based studies of flowering plants (Angiospermae) indicate a Triassic (or even Permian) origin (Martin *et al.* 1989), but no fossils yet date from prior to the Cretaceous (Cleal 1989).

The Jurassic was warm and humid, with no polar ice caps, and in many respects the Australian flora of this time resembled that of the other parts of the world. Conifers, cycads, pteridosperms and ferns were dominant. In Gondwana the conifer families Podocarpaceae and Araucariaceae made their first substantial appearance. Today these families are still confined predominantly to the Southern Hemisphere, although the Podocarpaceae occur also in Japan. The Araucariaceae are represented in present-day, Australian wet forests by *Agathis* and *Araucaria*. Larvae of the very 'primitive', south-western Pacific moth family Agathiphaeidae feed only on the seeds of *Agathis* (Robinson and Tuck 1976); an endemic Australian subfamily of cynipoid wasps (Austrocynipinae) (Chapter 42) is associated with the seeds of *Araucaria*; and a group of 'primitive' south temperate weevils (Nemonychidae: Rhinorhynchinae) feed on the pollen of Araucariaceae and Podocarpaceae (Kuschel 1983). Beetles of the subfamily Paracucujinae (Boganiidae) are restricted to the Cycadaceae, feeding on pollen as both larvae and adults; the South African *Metacucujus encephalarti* occurs in *Encephalartos*, while the Western Australian *Paracucujus rostratus* occurs in *Macrozamia* (Endrödy-Younga and Crowson 1986).

In the early Cretaceous a rise in sea levels coincided with cooling and the accelerated breakup of Gondwana. Massive marine incursions dissected Australia into isolated or semi-isolated eastern, western and northern land areas, and much of today's arid inland was inundated by sea. Northern regions possibly were drier than were southern ones. The flora was still dominated by the ferns, pteridosperms, cycads and conifers, but evidence of angiosperms first appears in the Australian fossil pollen record at c. 110 mybp (Truswell *et al.* 1987). As the Cretaceous became progressively warmer and the oceans receded from Australia, angiosperm diversification included radiation of the Proteaceae, Myrtaceae and Mimosaceae, plants which dominate in many present-day Australian communities and which together host a very large proportion of the Australian phytophagous insects (New 1988b).

Palaeocene (65–55 mybp) Australia, including the interior of the continent, was moist, with forest probably

widespread, at least in southern regions. The angiosperm flora was diverse and probably included a few xeromorphic elements related to present-day taxa such as *Banksia*, *Grevillea* and *Casuarina*. Xeromorphic (including sclerophyllous; see Seddon 1974) plants probably originated in impoverished soils on the periphery of rainforests, preadapted for the developing xeric conditions.

The Australian Eocene was also generally warm and humid but with several cooler, drier periods, and an overall temperature decline towards the end of the epoch. The continent was for a short time fragmented into islands. These climatic and topographic fluctuations may have stimulated speciation in plants and animals, and there is certainly fossil evidence of a strongly diversifying flora. The vegetation of northern Australia is unknown, although marshes must have been present in the southern N.T. The southern half of the continent was covered by widespread rainforests. The latter seem to have been mixtures or mosaics of tropical, subtropical and temperate forest plants, and may not have been like any present-day plant association. Mangroves grew along some southern shores. By the end of the Eocene, temperate podocarps and *Nothofagus* flourished in south-eastern Australia at the expense of tropical elements, although the latter may have persisted in the slightly warmer south-west.

In the early Oligocene (about 38 mybp) Australia became cooler and drier as a result of the development of a circum-Antarctic circulation of cold, marine currents to the south of Australia. Glaciation in Antarctica proliferated. The Australian fossil record is sparse but possibly the interior was more arid, providing conditions for the first proliferation of the Eremaean (see p. 196) flora, and the formerly widespread, podocarp-*Nothofagus* forests became restricted to southern, coastal fringes. It is likely that *Acacia* and Myrtaceae such as *Eucalyptus*, *Callistemon*, *Leptospermum* and *Melaleuca*, commenced their diversification during this epoch.

Warm, humid conditions returned in the Miocene (c. 25 mybp) and Australia was once again covered extensively by rainforests, both subtropical and temperate. By about the mid Miocene the continent was becoming increasingly, at least seasonally, arid. Large areas of grassland appeared. Gallery rainforests may have persisted in inland Australia around extensive lakes and rivers. A large fauna of terrestrial and arboreal marsupials, birds (including many species of flamingoes), crocodiles and freshwater fish flourished in the inland Lake Eyre–Lake Frome region. Asteraceae, which host a variety of phytophagous insects, first appear in Australia in the Miocene. Increasing aridity and reduction in temperatures in the late Miocene and Pliocene led to the eventual restriction of Australian rainforests to disjunct areas along the eastern margin of the continent. This pattern remains to the present, except where human activity has furthered the contraction. Miocene sea incursions may have been significant and an ocean barrier in the Nullarbor region is believed to be responsible for east-west sister groups at the specific and generic levels in various plant families, such as the Restionaceae, Epacridaceae and Myrtaceae.

The Quaternary (1.6 mybp to Present) was a period of

disruptive, climatic and environmental fluctuation. World-wide there were up to nine glacial-interglacial episodes in the Quaternary, each characterised by cool, dry periods of low sea level, followed by warm, moist periods when the polar ice sheets receded, freeing water for global rises in sea level. The periods of maximum warmth were relatively short and would not have allowed the full restoration of moist, warmth-dependent forests. During the glacial periods large areas of the continental shelf were exposed and Australia became broadly connected to New Guinea and to Tasmania. Glacial-interglacial fluctuations were mirrored in repeated contractions and expansions of rainforests and altitudinal oscillations in vegetation zones. Even during glacial maxima ice caps in Australia and New Guinea would not have extended beyond the high mountains.

Many biologists believe the climatic and environmental fluctuations of the Quaternary to have been of great significance in promoting speciation among insects. Periodic isolation of moisture-dependent taxa in pockets (refugia) of wet forest surrounded by inhospitable, drier vegetation is proposed as a major speciation mechanism (e.g. Keast 1961). Likewise, insects associated with dry sclerophyll vegetation may also have found themselves periodically dissected into isolated populations, sometimes by tracts of temporarily expanded wet forest, sometimes by equally ephemeral areas of great aridity extending outwards from the centre of the continent. However, as observed by Cracraft (1982), these suggestions have not been placed in a cladistic-vicariance context that allows determination of relative ages of these postulated Quaternary barriers. Furthermore, since refugia represent large scale survival of taxa during inclement times, one would expect congruent biogeographic patterns to result, but these are little investigated to date. Lynch (1988), in reviewing the kinds of evidence required to verify the existence of Pleistocene forest refugia, stressed the primacy of systematic data over the predominantly ecological explanations of, for example, Endler (1982). In the Northern Hemisphere, Pleistocene effects on the beetle fauna invoked little or no speciation but involved range shifts and extinctions (Coope 1979) that may cause great difficulty in biogeographic interpretation (Noonan 1988).

In New Zealand ice sheets covered much of the South Island and populations of insects, such as cicadas and diapriid wasps were isolated in small, unglaciated refugia around the periphery of the ice. Ice covered a much smaller percentage of land area in Quaternary Australia and hospitable, periglacial areas were not isolated from each other as were the New Zealand refugia. As a result, there is little evidence of periglacial speciation in Australia compared with New Zealand.

Substantial bodies of water persisted in inland Australia well into the Quaternary, but they became increasingly ephemeral. Today in these regions stream flow is highly unreliable, and the lakes are largely ephemeral. The final demise of the great vertebrate communities associated with these inland lakes and streams has taken place during human occupancy of the continent. During the last glacial period of low sea levels the

land connection between Australia and New Guinea featured a large, fresh to brackish lake which occupied much of the present-day Gulf of Carpentaria. At least in the second half of the Quaternary (by about 300 000 years ago) highly regular, sand dune systems were evolving in the extremely arid parts of inland Australia (Bowler 1976).

The land connection between the mainland and Tasmania has been broken and restored on numerous occasions since the Miocene. The final development of the Bass Strait and the inundation of the Gulf of Carpentaria, occurred within the past 10 000 years as sea levels rose following melting of the final Pleistocene glaciers. The present Torres Strait separating New Guinea from northern Australia is a similar development of the past 10 000 years (Doutch 1972) following a probably prolonged, Quaternary connection between New Guinea and northern Australia (Kikkawa *et al.* 1981).

The development of upland areas on the continent is not very clear. Throughout the Mesozoic and early Tertiary much of the exposed land was relatively flat with lakes and relatively slow-flowing rivers (Laseron 1969), and low-lying land was prone to inundation by rising sea levels. However, mountainous regions existed during the Palaeozoic. Orogeny in New Guinea commenced at the time of the mid-late Miocene tectonic collision and continued throughout the Pliocene: a true alpine zone with glaciation is present there today. However, it is uncertain whether a distinct alpine zone has existed continuously in mainland Australia and Tasmania since the Palaeozoic, or since the time of some late Cretaceous mountain building, or only since the Pliocene uplifting and vulcanism, which resulted in the present-day peaks, ranges and tablelands of the Great Dividing Range. Lambeck and Stephenson (1986) date the orogeny of the Great Dividing Range to a minimum of 20 mybp and Costin *et al.* (1979) believe the Kosciusko area to have reached its present elevation during the Tertiary. The restriction to cool running waters of aquatic insects with close Gondwanan affinities such as some Diptera [Chironomidae (Brundin 1966) and Blephariceridae (Zwick 1977b)], Ephemeroptera (Campbell 1981), Plecoptera (Zwick 1979a) and Trichoptera (Neboiss 1977) strongly suggests that appropriately elevated areas with cool, lotic systems have been present on the Australian plate since the Jurassic-Cretaceous fragmentation.

Some difficulties in interpretation and reassessment of previous views on the biogeography of alpine areas in Pleistocene to recent times are discussed for Tasmania by Kirkpatrick (1986) and for south-east mainland Australia by Kershaw *et al.* (1986). The lack of pollen deposits in upland areas is a disadvantage, although De Deckker (e.g. 1986) has demonstrated the suitability of fossil and sub-fossil, non-marine ostracods from lacustrine sediments in reconstructing Pleistocene climates.

The Significance of Palaeontology to Biogeography

Just as palaeontology was considered to be central to phylogenetics (Chapter 4), it has been argued that it is central

to biogeography in the determination of historic distribution patterns and processes. Many biologists state that the biogeography (and evolutionary history) of their study group cannot be reconstructed because of the lack of fossils. As seen above, biogeographic reconstruction does not rely on, or even require, a knowledge of fossils. Although palaeontology provides the only direct evidence of past biotic distributions, the imperfections and incompleteness of the fossil record is well known (Chapter 6). With the development of phylogenetic reconstruction through cladistics (Chapter 4) and the development of vicariance methods of biogeographic analysis, some palaeontologists such as Patterson (1981b) considered that fossils were too often uninformative, providing too few characters for analysis, or too vague in their relationships to other fossil and extant taxa. Furthermore, assumptions that the site of the oldest fossil of a group or the most 'primitive' member marked its centre of origin were challenged as untenable.

Grande (1985), though accepting many of the reservations concerning the primacy of palaeontology, argued that fossils could (i) provide new morphological and ontogenetic data for systematics, (ii) provide additional taxa to add to the known range of a higher taxon, (iii) establish the minimum age for a taxon, and (iv) allow analysis of biogeographic patterns from a different time than the Recent.

As far as insects are concerned, some of Patterson's reservations are removed with the excellent preservation of fossils in amber (e.g. Larsson 1978; F. M. Carpenter, in press). Fossiliferous amber dates from the Lower Cretaceous (Neocomian) of Lebanon through the Upper Cretaceous of Canada and Siberia, the Eocene–Oligocene of the Baltic, the Miocene of Saxony, Sicily and Mexico to more Recent copal. Amber is rarely present in the Southern Hemisphere, but Lebanon may have been part of the northernmost margin of Cretaceous Gondwana (Brundin 1976; Cranston *et al.* 1987). With few exceptions (e.g. Koteja 1986), those who study amber have not been fully cognisant with modern faunas, and, likewise, those who study recent faunas have been less than diligent in examining appropriate amber material. Examples of the use of such entomological material in austral, biogeographic analyses and in providing confirmation for the vicariance-based dating of clades include Munroe (1974), Brundin (1976) and Cranston *et al.* (1987). Furthermore, reliably identified fossils can test models of vicariant biogeography based upon extant taxa alone. For example, fossil evidence of presently exclusively Gondwanan taxa from post-Cretaceous (*i.e.* post break-up), non-Gondwanan sediments, would require re-examination of an austral-vicariance hypothesis.

Biogeographic Regions within Australia

The conflict between ecological and historical explanations for world-wide, disjunct distributions is repeated on the finer continental and regional scales. Classically, Australia has been divided into three zones: the Torresian, Bassian and Eyrean zones of Spencer (1896). In her phy-

logeographic analysis, Burbidge (1960) recognised three principal zones, the Tropical, Temperate and Eremaean, with close match to the regions of Spencer, but with additional recognition of smaller areas of high endemism and/or diversity, namely North Queensland, the Macpherson–Macleay overlap, south-western Australia and Tasmania. With the addition of Tumbunana and Irian zones in New Guinea and northern Australia by Schodde and Calaby (1972), these regions are widely recognised as a means of simplifying and communicating patterns of biotic distribution (Nix 1982). However, the biogeographic regions and subregions are essentially unquantified descriptions of relative biotic similarities and differences (the results of historical structuring processes) and are non-hierarchical, lacking explanation of their relationships or origins.

Nix (1982) attempted a bioclimatic classification of the Australian plate, seeking to explain the distributional patterns observed. Nix found environmental determinants, particularly thermal responses (characterised as mega-, meso- and microthermal) to be primary determinants of present day (and past) distribution patterns. His bioclimatic zones bore strong resemblance to those previously recognised by Spencer and Burbidge.

Vicariance biogeographers have endeavoured to discover the historical relationship between well known, Australian areas of endemism. Cracraft (1982), utilising data from bird studies (Fig 7.11B), proposed a general hypothesis (Fig. 7.11A) as follows: (i) major separation (by barrier F) of a northern + eastern avifauna from the central + southern elements, (ii) development of a broad barrier (G) separating the arid centre and the entire mesic south, (iii) bisection of the central (by H) and southern (by I) faunas. In the north, a western fauna was divided (by D) from a north-eastern and eastern component, with subsequent development of barriers E, B, C, then A. Cracraft observed that many of these barriers have been related to Pleistocene climatic deterioration and habitat discontinuities, but neither cladistics nor vicariance nor relative ages of the barriers have been discussed previously. The general hypothesis still requires testing by congruence with other taxa for the areas concerned.

Botanists (e.g. Ladiges and Humphries 1986; Weston and Crisp 1987; Thiele and Ladiges 1988) have produced area cladograms for taxa occurring on the east coast of Australia, finding congruence of vicariance associated with the Macpherson–Macleay overlap and a coastal/tableland event in New South Wales. Comparable entomological studies are rare, but the significance of the Macpherson–Macleay overlap is evident, for example in Odonata (Watson and Theischinger 1984a) and Tabanidae (Mackerras 1962).

The Future

Future Australian biogeographic studies should be grounded in good systematics, take cognisance of extralimital distributions, and not be constrained by current dogma of earth history. Non-standard, geological theories that require testing in this region are the expand-

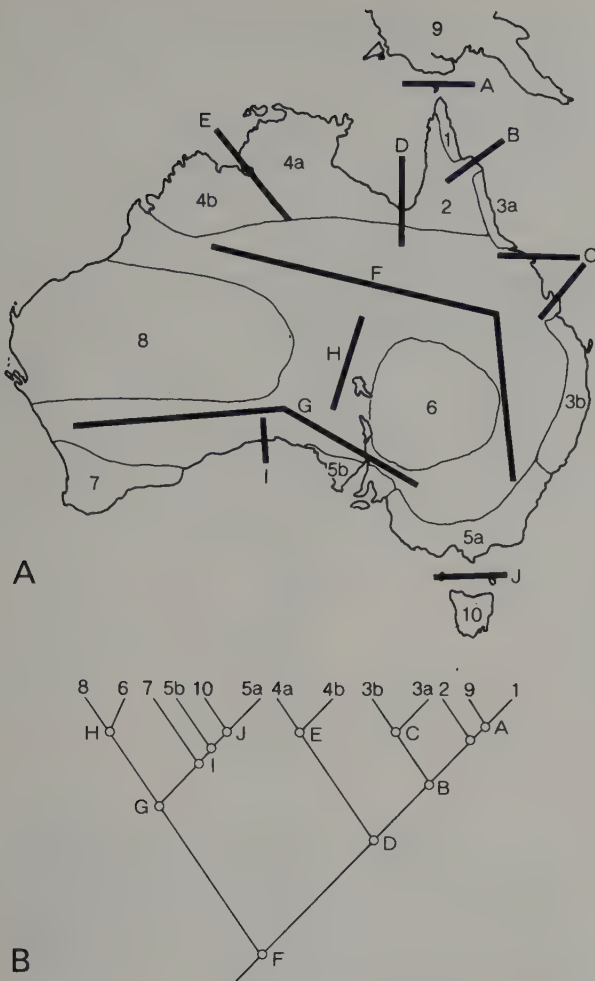


Fig. 7.11 Vicariance hypothesis for Australian areas of endemism based on cladistic relationships of bird taxa. Letters A–J refer to postulated vicariance barriers (see text). [After Cracraft 1982]

ing earth hypothesis (see above), complex, hybrid origins for New Zealand (e.g. Craw 1988) and the existence of a previous continent of Pacifica (Nur and Ben-Avraham 1981; Humphries and Parenti 1986). The latter hypothesis may account for some of the amphotropical distributions observed above. Theoretical developments must include tests for dealing with incongruence arising when different histories are overlaid and for estimating the reliability of area cladograms.

The major factor affecting the distribution of the Recent Australian biota has been the dispersal of *Homo sapiens*. The introduction of non-native animals and plants (Thomson *et al.* 1987), the alteration of native habitats through the increased frequency of fire (Singh *et al.* 1981) and the destruction of other habitats through, for example, the clearing of forests, draining of swamps and alteration in the water table. All of these changes must have had a more profound effect on the native biota than most of the geophysical events of geological time.

The future of the Australia biota is similarly dependent upon human activity. If global warming occurs due to continued emission of various gases (the 'greenhouse' effect), the biota will respond by range contraction and extinction of cold stenotherms (microthermic *sensu* Nix 1982), range expansion of warm stenotherms (macrotherms) and range changes of the warm eurytherms (mesotherms). These results and those associated with an elevation of sea level can lead only to a further reduction in biological diversity by *Homo sapiens*.

ACKNOWLEDGMENTS. We are indebted to many Canberra colleagues including G. Young, D. Faith, M. Crisp and P. Weston, for comments on geographical, geophysical, botanical and zoological matters discussed in this chapter.

Biographical History

E. N. MARKS

The history of Australian entomology has been variously divided into periods. Musgrave (1930) considered three which he named after leading taxonomists: Fabrician (1770–1830), Westwoodian (1831–61) and Macleayan (1862–1929). W(hitley) (1961) suggested adding to Musgrave's three periods, a fourth, Musgravian (1930–59). Mackerras (1949) recognised four periods (Table 8.1): the Period of Exploration (1770–1860); the Macleayan Period (1861–90); the Period of the Amateurs (1891–1927); and the Period of the Professionals (1928–). He commented: 'It is to be emphasised that these four periods are by no means sharply separated; each overlaps, sometimes widely, the period on either side, but each is distinguished by a central influence which is easily recogni[s]ed'.

The rationale for these periods will be apparent in what follows, although they are not the basis for arrangement of this chapter. The cut-off dates for Mackerras's periods approximate significant events in Australian entomology: foundation of the Entomological Society of N.S.W. in 1862 and of its journal in 1863; appointment of the first government entomologists, C. French Snr in Vic. in 1889 and A. S. Olliff in N.S.W. in 1890 (not perhaps appropriate to start the Period of the Amateurs); Nicholson's (1927) study of mimicry, which in Whitten's view (see Chapter 10) marks the beginning of entomological science in Australia; and foundation of the Division of Economic Entomology of the Council for Scientific and Industrial Research in 1928.

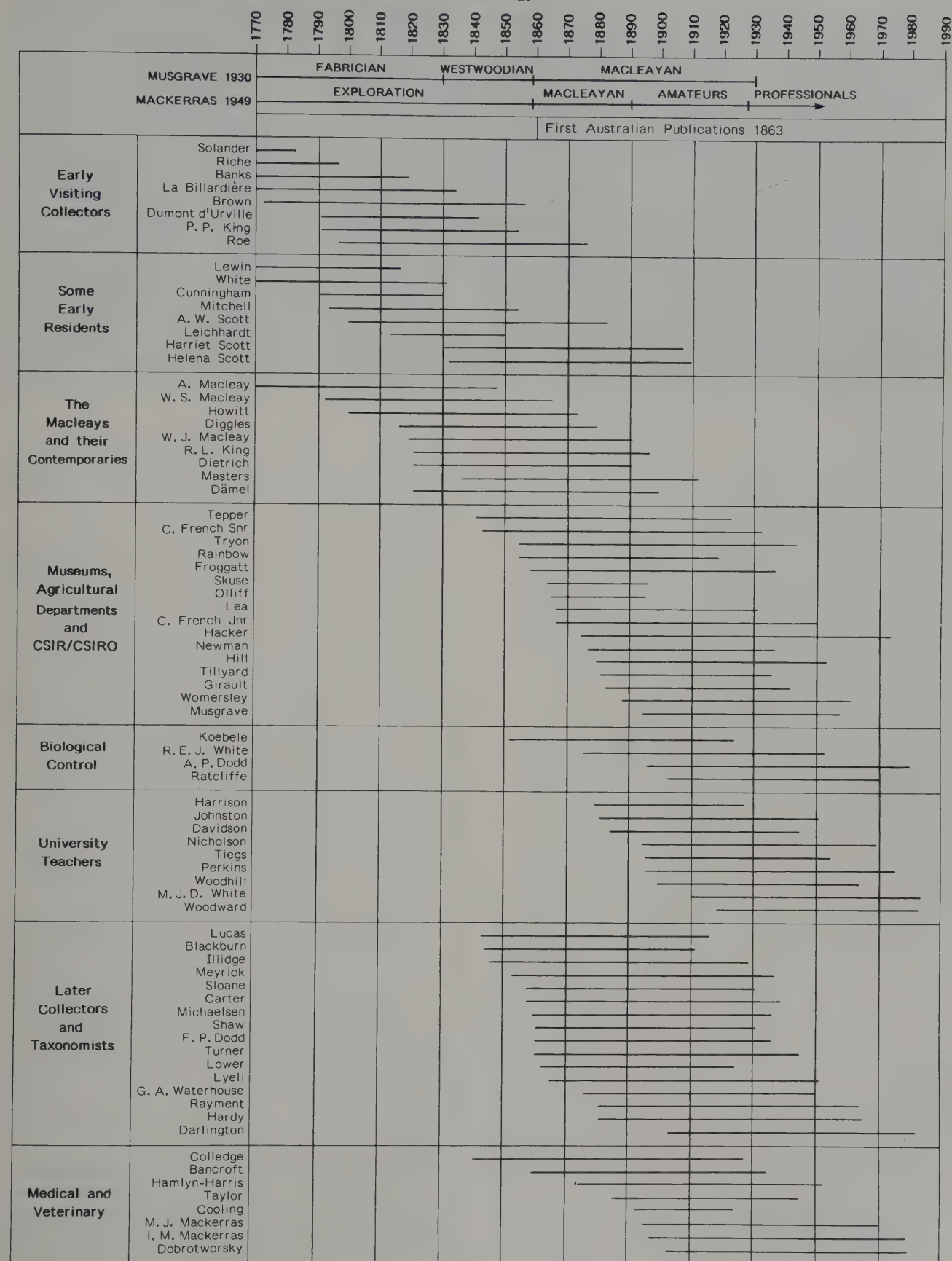
In broad terms, Australian entomology began in 1770 and continued after 1788 with collection of insects by visiting naturalists and description of them by entomologists

in Europe. Collecting by local residents gradually increased but not until 1863 were descriptions published in Australia (W. J. Macleay 1863–64). This pattern has persisted but now the proportion of visiting collectors is small and most systematic papers are published in Australian journals.

The earliest entomologists resident in Australia were amateurs or paid collectors. The 1880s and 1890s saw appointment of professional entomologists (most of them with practical, non-academic training) in museums and departments of agriculture, development of medical entomology, and use of Australian insects for biological control of insect pests. In the 1910s and 1920s introduction of insects to control introduced weeds was established, and measures begun for mosquito control. In the 1920s governments began to employ university graduates as entomologists and universities appointed lecturers in entomology; general principles, as distinct from practical problems, came under study, and the Commonwealth Government confirmed its interest in economic entomology. After the 1939–45 war, entomology expanded on all existing fronts and on some previously scarcely touched, such as genetics, biochemistry, physiology, ecology, behaviour, insecticide resistance and transmission of viral diseases to man and animals.

So many individuals have contributed to knowledge of Australian insects that a biographical history of Australian entomology must be very selective, perhaps unfairly so. In order to reduce the field, biographical notes are here limited to deceased entomologists who have actually worked in Australia, although others are mentioned where appropriate. References to those active

Table 8.1 Life spans of some major figures in Australian entomology



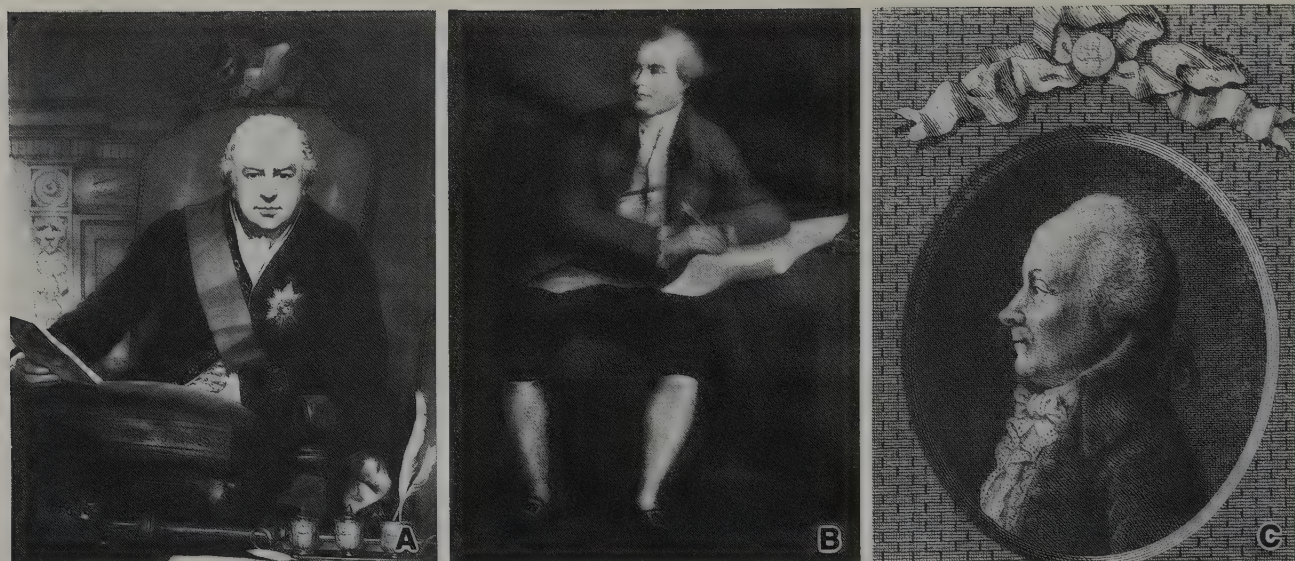


Fig. 8.1 A, Joseph Banks; B, Daniel Carl Solander; C, Johann Christian Fabricius.

before 1930 can be found in Musgrave (1932) which has been drawn upon extensively throughout this chapter. Accounts of collecting expeditions are given in Musgrave (1930) and Whittell (1954) and some taxonomists are treated in Marks (1983a). There are many entries of Australian interest in P. Gilbert's (1977) world compendium of biographical literature on entomologists. The background history of world entomology can be found in R. F. Smith *et al.* (1973) and Moyal (1986) has provided a vivid sketch of science in general in eighteenth and nineteenth century Australia.

Early Visiting Collectors

During the eighteenth century, the wealthy in Holland, France and England were tremendously interested in growing new plants brought back from their countries' colonies and voyages of exploration; some also owned private zoos, museums and insect collections.

Carolus Linnaeus (1707–78) (Blunt 1971), who from 1741 was Professor of Medicine and Botany at the University of Uppsala, Sweden, published the 1st edition of his book *Systema Naturae* in 1735 (modern zoological nomenclature dates from the 10th edition in 1758). By 1746 he had recognised seven orders of insects using wings as the basis for his classification. His binomial system of nomenclature created a great upsurge of interest in the naming of plants and animals and stimulated collecting wherever Europeans travelled. He was a superb teacher and gave his students a broad grounding in mineralogy, botany and zoology, with plenty of field work, and instilled in them habits of order and accuracy. Two of his students influenced the birth of Australian entomology.

Although insects were mentioned by earlier voyagers (see Chapter 9), the first real contribution to knowledge of the Australian insect fauna resulted from the collections made by Banks and Solander during the voyage of the *Endeavour* along the east coast in 1770. It is not generally appreciated that Solander was a university-trained,

professional entomologist, although entomology was but part of his natural history training and professional expertise. Indeed, botany was his predominant interest during and after this voyage.

Daniel Carl Solander (1733–82) (Rauschenberg 1968) was a Swedish parson's son who in 1750 entered the University of Uppsala to study law. However, when he took Linnaeus's course in Natural History he became fascinated and switched to science subjects aiming for a medical degree. He was a favourite pupil of Linnaeus and assisted him in classification of the Swedish royal collections, which included 'an unbelievable quantity of pinned insects'. He arrived in London in June 1760, sent by Linnaeus to catalogue the plants in his friend Peter Collinson's garden according to the Linnean system. Starting at the British Museum as an assistant in 1763, he spent five years cataloguing its natural history collections, becoming Assistant Keeper in 1765 and Keeper in 1773. Concurrently he helped classify some important private collections. He was elected a Fellow of the Royal Society in 1764.

Solander was short and stout, an interesting and amusing conversationalist and gifted linguist, with agreeable, unassuming manners. He was quickly accepted into London's social and intellectual circles, and gave generous assistance to other naturalists in classifying and helping to describe their specimens. James Smith, first President of the Linnean Society, looking back in 1821, said of him 'His instruction made everybody correct and systematic and introduced Linnean learning and precision' and his 'talents and liberality . . . proved the example and the spur of all that has been done for natural science, during half a century, in Britain'.

Joseph Banks (1743–1820) (Beaglehole 1962), as a boy at Eton, became interested in the local wild flowers and insects. At Oxford University he obtained permission to employ a Cambridge botanist as his private tutor. When he inherited large estates in Lincolnshire, he decid-

ed to devote his leisure to natural history. In 1766 he was elected a Fellow of the Royal Society and travelled in HMS *Niger* to Newfoundland and Labrador, where he collected rocks, plants and animals. Solander gave him botanical advice before he left and helped him catalogue the plants on his return.

When the Admiralty agreed to the Royal Society's request for a ship to take scientists to Tahiti to observe the transit of Venus in 1769, Banks's offer to finance a team of naturalists on the voyage was accepted. Banks related how he and Solander were at a dinner party 'talking about how I had an unmatched opportunity to enrich science and to become famous, Solander all at once excitedly . . . asked me . . . would you like a fellow-traveller. I answered: someone like you would give me untold pleasures and rewards. Then that is it, he said, I'll travel with you; and from that moment everything was settled and decided'. The spring and summer of 1768 were spent in preparation for the voyage. Stearn (1974) 'feels that Solander contributed immeasurably to the success of the voyage not only through his methodical industry and his scientific learning but also through his genial and easy-going disposition'. When they returned in 1771, Solander became Banks's librarian and curator in addition to his outside activities; he died from a stroke in 1782.

A Danish pupil of Linnaeus, Johann Christian Fabricius (1745–1808) (Hope 1845; Tuxen 1973), who was developing a system of insect classification based on mouth-parts, came to London in 1767. Solander introduced him in scientific circles and he identified and described specimens in many collections. The following year, he helped Banks and Solander prepare their quarters on the *Endeavour*. Their equipment included 'all sorts of machines for catching and preserving insects'. On their return, he studied the insect collection made in 1770, along the east coast of Australia, and in *Systema Entomologiae* . . . , published in 1775, described 212 species (in 10 present day orders) from New Holland. This was the first publication on Australian entomology.

Banks was 'good-humored, liberal, a tolerable botanist, and generally acquainted with natural history'. His forte was administration. King George III appointed him special adviser and unofficial director of the Royal Gardens, Kew, in 1773 and his personal friendship with the king was a factor in his election as President of the Royal Society in 1778, for the previous president had aroused the king's displeasure. He held this office until his death in 1820. Through his influence in high places, his great wealth and his abiding interest, he became the first great patron of Australian natural history, and gave encouragement and practical and financial support to many collectors.

The widespread interest generated by the natural history collections of the *Endeavour*'s voyage facilitated appointment of naturalists to accompany the later voyages of exploration by both French and English. They were sometimes members of the ship's company, or were passengers supported by government institutions or private patrons. Stanbury (1987) comments: 'In general, the early French zoological work on Australia's fauna was carried out

much more consistently and competently than that by the English'. This may be a reflection of Banks's predominant interest in plants or of the 'humiliating picture of the state of zoological instruction in Great Britain' where *circa* 1820 there was no zoological chair in any university and only three professors of Natural History compared to thirteen, with their numerous assistants, in Paris (W. S. Macleay, quoted by Fletcher 1921).

Among the scientists Fabricius met on a visit to Paris in 1790 were Claude Antoine Gaspar Riche (1762–97) and Jacques-Julien Houton de La Billardière (1755–1834) (Maiden 1910). Riche, who had abandoned his university studies because of ill-health, was mainly interested in insects. La Billardière was a doctor of medicine, and a distinguished, much-travelled botanist. In 1791 these two sailed as naturalists on the expedition led by Bruny d'Entrecasteaux in search of La Perouse. They collected in W.A. and Tas. Near Esperance, in December 1792, Riche was lost in the bush for 54 hours, surviving on fruits of a *Leucopogon* which La Billardière collected and subsequently named *Leucopogon richiei*. The two ships reached Java in October 1793, but before this both commanders had died. The officers who took over were royalists and when they heard of the death of Louis XVI, they handed their ships to the Dutch. Riche died of consumption on his return to France. La Billardière, who was a republican, was imprisoned in Batavia for 18 months. In 1795 the collections were sent to England as a prize of war after the Dutch ship taking them to Europe was captured by a British warship (H. B. Carter 1988). Banks used his influence to have the collections returned intact to the French. He told the French botanist Jussieu that he would have been afraid of stealing even one single botanical idea from a man who had collected them at the peril of his life. Between 1801 and 1805 Fabricius described numerous insects from these collections.

Among many other French collectors, Jules Sebastien-César Dumont d'Urville (1790–1842) (Anon. 1983), naval officer and navigator, was on three voyages to the Pacific that touched Australia, in 1823–24, 1826 and 1839. On the first, in *La Coquille*, as no naturalist had been appointed, the officers apportioned responsibility and d'Urville, the second officer, 'took upon himself botany and entomology'. On the second, in command of *L'Astrolabe*, he collected at King George Sound (W.A.). A. White (1841), who described insects collected there by Captain George Grey, wrote of him as 'Admiral d'Urville who seems to unite the seemingly incompatible duties of a commander of an expedition with an enthusiastic love of and search for insects'. D'Urville had then just returned from a voyage 1837–40 'au Pole Sud et dans l'Océanie'. He was burnt to death in a railway accident in 1842. His insects were described principally by Boisduval, Blanchard and Le Guillou, some in the lavishly illustrated, multi-volume accounts of d'Urville's voyages.

Among the naturalists on British ships was Robert Brown (1773–1858) (Burbidge 1966; Stearn 1974). Best known as a botanist, Brown was a Scottish parson's son, tall, reserved and endowed with a dry wit. He studied

medicine at Edinburgh University and showed a special interest in natural history which continued after he became an army surgeon. He so impressed Banks, whose herbarium and library he visited in 1798, that Banks offered him the post of naturalist on HMS *Investigator* which sailed in 1801 under the command of Matthew Flinders and made a detailed survey (1801–03) of unexplored parts of the Australian coast. Brown was paid by both the Army and the Admiralty. After collecting in N.S.W. and Tas. he returned to England in 1805. Of the insects collected, 33 species were described by W. Kirby and others by W. S. Macleay (see p. 203), who also described insects from the four survey voyages (1817–22) commanded by Lieutenant P. P. King in the *Mermaid* and the *Bathurst*. These surveys were mainly of the north-west coast. Insects were collected by at least three of the ship's company, King, Roe and Cunningham. Phillip Parker King (1791–1856) (Anon. 1967) who had broad natural history interests, was born on Norfolk Island where his father was Lieutenant-Governor, grew up in England, and was trained as a naval hydrographer; he became the first Australian-born Fellow of the Royal Society in 1824. John Septimus Roe (1797–1878) (Uren 1967), an English parson's son, was posted as Master's Mate to the survey. Later, when he became the first Surveyor General of W. A., he continued to send insects to England for description by F. W. Hope, J. O. Westwood and others.

The 'official' naturalist on King's surveys was Allan Cunningham (1791–1830) (McMinn 1970), the London-born son of a Scottish gardener. He had worked as a clerk to the curator of the Royal Gardens, Kew, where he met Robert Brown. He was appointed a botanical collector to the Royal Gardens on Banks's recommendation and arrived in Sydney in 1816. A. White (1841) commented that Cunningham 'gathered a rich harvest of rare and unknown (insect) species on the north-west coast of Australia'. He collected insects also on his later inland explorations in eastern Australia.

Some Early Residents

Residents of the young colony collected insects for their own interest, or to send to friends, to exchange or sell.

John White (1756?–1832) (Rienits 1967b), Chief Surgeon of the First Fleet, was a keen naturalist who resided in Sydney from 1788 to 1794. He gave insects to John Francillon, a London doctor who had a celebrated collection almost half of which was purchased in 1818 by Alexander Macleay (see p. 203).

John White is well known for his illustrated book *Journal of a Voyage to New South Wales* . . . , published in London in 1790. In 1792 White had assigned to him a servant Thomas Watling (b. 1762) (Rienits 1967a), a newly-arrived convict who was a well-educated Scottish artist transported for forgery. He made many drawings for White and was given an unconditional pardon in 1797, later returning to Scotland. The 'Watling Collection' in the Zoological Library of the British Museum (Natural History) comprises 512 drawings made between 1788 and

1794 by various artists (Smith and Wheeler 1988); 123 are signed by Watling and many bear annotations by John White. This collection includes some of the oldest known illustrations of Australian insects in their natural habitat. Another artist naturalist, John William Lewin (1770–1819) (Mander-Jones 1967) was an engaging character who arrived in Sydney in 1800. Patrons in England, including Alexander Macleay, helped to support him in return for natural history specimens. His first book was published in London in 1805: *Prodromus Entomology. Natural History of Lepidopterous Insects of New South Wales* . . . The 18 plates were engraved by Lewin in Parramatta, the copper plates and paper having been provided by the English entomologist Dru Drury; they were the earliest engravings of any kind produced in Australia. Lewin sent them to his brother Thomas in London together with notes for the text. Thomas went to the Linnean Society for advice. The President, James Smith, identified the food plants as far as possible, and the Secretary, Alexander Macleay, drew up scientific descriptions of the insects. These seem to be the only insects Alexander Macleay described, though the names are attributed to Lewin.

In 1830 or 1831, Adolphus Schayer (Erichson 1859; Marks 1955) a Silesian wool expert, came to Tas. with a consignment of Saxon Merino sheep for the Van Diemen's Land Company; later he was superintendent of its station 'Woolnorth' on the north-west coast. He sent to Berlin 'three assortments of carefully selected insects' from which Erichson in 1842 described 262 new species. The fact that 'these collections are not confined to the larger and more remarkable varieties, but they embrace also the most insignificant' enabled Erichson to discuss the zoogeography of the 'New Holland Fauna'.

Some of the overland explorers collected insects, among them Sir Thomas Livingstone Mitchell (1792–1855) (Foster 1985), a Scottish soldier and veteran of the Peninsular war, who was Surveyor General of N.S.W. in 1828–55. He gave a 'considerable collection' made on his 1846 expedition to the districts of the Maranoa and Barcoo Rivers, to his friend W. S. Macleay, including Coleoptera that were described by W. J. Macleay during the 1860s. In his journal (1847) the Prussian explorer-naturalist Ludwig Leichhardt (1813–?50) (Roderick 1988), interrupts the account of his search for the way down the precipitous Arnhem Land escarpment, with observations on the spectacular, blue and red grasshopper *Petasida ephippigera*, which he found there among the rocks.

A fine, illustrated folio volume on Lepidoptera was in preparation during the 1840s by A.W. Scott and his daughters (Gray 1976; Ord 1987, 1988) and was reviewed in 1851 in the *Sydney Morning Herald* as 'soon to be published'. Alexander Walker Scott (1800–83), MA of Cambridge and son of a distinguished physician-botanist, first came to Australia in 1827. He established businesses in Newcastle and farms at Maitland and on Ash I. in the Hunter River. He was a talented artist and keen naturalist (the explorer Leichhardt commented on his sharp eyes). From 1846 to 1866 he lived at Ash I. where he educated his daughters, Harriet (1830–1907; m. Morgan) and

Helena (1832–1910; m. Forde), and launched them on their careers as professional artists and natural science collectors and illustrators.

Eventually Volume 1 of *Australian Lepidoptera and their Transformations* . . . was published in England in 1864. Volume 2, edited and revised by A. S. Olliff and Helena Forde, was published by the Australian Museum in five parts, 1890–98. Most of the plates in these volumes colourfully depict adult moths or butterflies, larvae and host plants, clearly drawn from living specimens, sometimes against romantic woodland or castle-turreted backgrounds.

The Macleays and their Contemporaries

The role that Banks had played in England until 1820 in providing stimulating encouragement and generous support to Australian natural history, was filled from 1825 to 1890 by three members of the Macleay family in Sydney. Before coming to Australia, the two elder, Alexander Macleay (1767–1848) and his son William Sharp Macleay (1792–1865) (J. J. Fletcher 1921; Strahan 1979; Horning 1984; Stanbury and Holland 1988) were senior British public servants and scientists of international repute; Alexander was a Fellow of the Royal Society.

Alexander Macleay was a Highlander from Caithness. He joined the British civil service and retired on a pension in 1818 after the Transport Board, of which he was Secretary, was abolished. In 1825 he accepted appointment as Colonial Secretary of N.S.W., a post he held until 1836. Described by his friend Robert Brown as a general naturalist, a profound entomologist, and a practical botanist, he was Secretary of the Linnean Society [of London] for 27 years from 1798. He never published on entomology but brought with him to Australia 'the finest and most extensive (insect) collection then existing in the possession of a private individual'. It had been built up by his own and his son's collecting, by exchange, and by purchase from at least six famous collections.

In Sydney, through his enthusiasm and influence, he was instrumental in the establishment of the Australian Museum in 1827. He sent natural history specimens, including insects, to the Linnean Society, but his little spare time was devoted to developing a garden of native and exotic plants on 54 acres (22 hectares) at Elizabeth Bay granted to him in 1828. By 1841 this had become 'a botanist's paradise' according to the botanist, J. D. Hooker.

Elizabeth Bay House, completed in 1837, with the insect collection and garden, was for half a century a focal point for local and visiting naturalists, who were welcomed by its kindly hosts Alexander, William Sharp who lived there from 1839, and William John who leased it after the latter's death.

W. S. Macleay, who inherited the Elizabeth Bay property and the collection, was educated at Westminster School and Cambridge University. He was attached to the British Embassy in Paris for about 10 years, where he made friends with leading French naturalists including Cuvier and Latreille who gave him a good grounding in taxonomy. After serving in Cuba from 1825 to 1836 as

Commissioner and Judge of the Mixed British and Spanish Court of Commission for the Abolition of the Slave Trade, he retired with a pension in 1837, and took an active role in British scientific societies. He was a general zoologist and his taxonomic papers (including those describing Australian insects collected by R. Brown and P. P. King) were a means to an end, for he was interested in philosophical aspects of animal classification for which he had proposed a circular and quinary system. In Cuba, he started his own zoological collection, principally of insects, and increased it by exchange and purchase. He brought the collection with him to Sydney in 1839 where he continued to add to it, though he published nothing further on entomology. At his death, his and his father's collections combined included 100 000 to 150 000 insects. He was an active trustee of the Australian Museum. His friend, Robert Lowe, a journalist and politician, described him thus: 'He was an excellent classical scholar, he knew more of modern history and biography than anyone with whom I was ever acquainted, and in addition to all this he was a profoundly scientific man, thoroughly conversant with zoology and entomology. An excellent companion with a store of caustic wit'. He must have been a stimulating shipmate for his cousin William John Macleay (1820–91) on their voyage to Australia in 1839.

W. J. Macleay (henceforth referred to as William) (J. J. Fletcher 1893, 1929), another Highlander from Caithness, on his Uncle Alexander's advice gave up medical studies at Edinburgh University to come to N.S.W., where he was fully occupied for many years in becoming a successful pastoralist in the Murrumbidgee area. He entered parliament in 1855. In 1864, returning from Wagga Wagga in his buggy, he came upon the bush-rangers Gilbert, Hall and Dunn 'sticking up' several teams and travellers. With rifle in hand he raised the siege, which earned him a gold medal for gallant and faithful services. From 1857 he made his home in Sydney, renewing a close association with W. S. Macleay. He began to build up his own collection of Australian insects and in 1862 became the first President of the Entomological Society of N.S.W., which published two volumes of *Transactions*, each of five parts (Vol. 1, 1863–66, Vol. 2, 1869–73). This, the first specialist scientific society in Australia, was initially very active but the entomological community was too small and scattered to maintain a specialist society; it last met in 1873 and was succeeded in 1874 by the Linnean Society of N.S.W., which embraced zoology, botany and geology (Marks and Mackerras 1972). Again William Macleay was its first President: he gave both societies generous financial support and published extensively in their journals, mainly on Coleoptera. He inherited Alexander and William Sharp Macleay's collections in 1865 and greatly increased the holdings by employing collectors. In 1874, acceptance of his offer to bequeath the combined Macleay collections to the University of Sydney (if a suitable building were provided) prompted William to leave parliament and concentrate on natural history and improvement of the museum. The Macleay Museum collection, which was actually

given to the University in 1888 prior to William's death, with later additions and losses, is estimated to include at least 500 000 insects (Horning 1984).

William Macleay was followed as President of the Entomological Society of N.S.W. by R. L. King and A. W. Scott (see p. 202). Robert Lethbridge King (1823–97) (Cable 1974), son of Phillip Parker King (see p. 202) grew up in Australia, graduated BA from Cambridge in 1846 and was ordained in the Church of England in Sydney in 1848. He contributed numerous papers, mainly on Coleoptera, while he was the incumbent of St John's, Parramatta (1855–67), but after he became principal of Moore Theological College in 1868 he had no leisure for entomology. He recorded the collectors of the specimens he described, including Dr G. Howitt to whom he was indebted for 'almost all that I know of the entomology of Victoria'.

Godfrey Howitt (1800–73) (M. H. Walker 1972) graduated MD (Edinburgh) in 1830 and practised as a physician in Nottingham, where he was well known as a botanist and entomologist. He arrived in Melbourne in 1840 where he made a large garden and was a founder of the Philosophical Society of Vic. in 1854. His insect collection, presented to the University of Melbourne, is housed in the Museum of Vic.; he did not publish on Australian insects but sent many to specialists abroad for naming.

William Macleay described two new beetles sent to him by Silvester Diggles (1817–80) (Marks 1963) who had a piano-tuning business and taught music and drawing. Born in Liverpool, Diggles arrived in Sydney in 1853 where he visited W. S. Macleay and sketched a moth in the collection. He moved to Brisbane in 1854. He was a keen collector of butterflies and beetles and began working out their life histories. He was a founder of the Qld Philosophical Society in 1859, and contributed specimens to the nascent Qld Museum which the Society founded in 1862. In 1871, he provided the first record of the wanderer butterfly *Danaus plexippus plexippus* in Australia and

suggested introduction of insects to control foreign plants. Many specimens were sent to the British Museum and later to a London 'Natural Agency Office' run first by Stevens and later by E. Higgins.

Diggles was anxious to have rare species described. He kept good drawings of them and acknowledged that Higgins was liberal in returns (foreign specimens, pins and pamphlets), commenting that William Macleay would probably be glad to describe a specimen but would expect it to be presented to him. Diggles gave great encouragement to the amateur collectors who sent insects to him but his chief correspondent was George Masters, who visited Brisbane several times.

George Masters (1837–1912) (Whitley 1974) was the son of an English gardener and became a gardener himself. Arriving in Melbourne about 1856, he was employed by Dr Godfrey Howitt, who probably stimulated his interest in entomology. By 1860 he was working as a gardener in Sydney. William Macleay sent him to collect at Port Denison, Qld, in 1862. He joined the Entomological Society of N.S.W. and frequently exhibited large collections of insects; the neatness of his mounting was much admired. In 1864 Masters was appointed assistant curator and collector to the Australian Museum on condition he sold his private collection and made no new one, an agreement he ignored. He was a fearless bushman and during field trips to many parts of Australia he collected also for Macleay. In 1874 he became curator of the Macleay Museum, a post he held until his death. With good intentions, he set about reorganising and relabelling the collection. Unfortunately, large numbers of original labels were discarded, so that today many specimens of historical or nomenclatural importance cannot be recognised. Masters published a 'Catalogue of described Coleoptera of Australia' but his great knowledge of habits and life histories was never recorded.

About 1861, William Macleay purchased 'a fine collection' of insects taken at King George's Sound by Edward Dämel, a German who travelled widely in

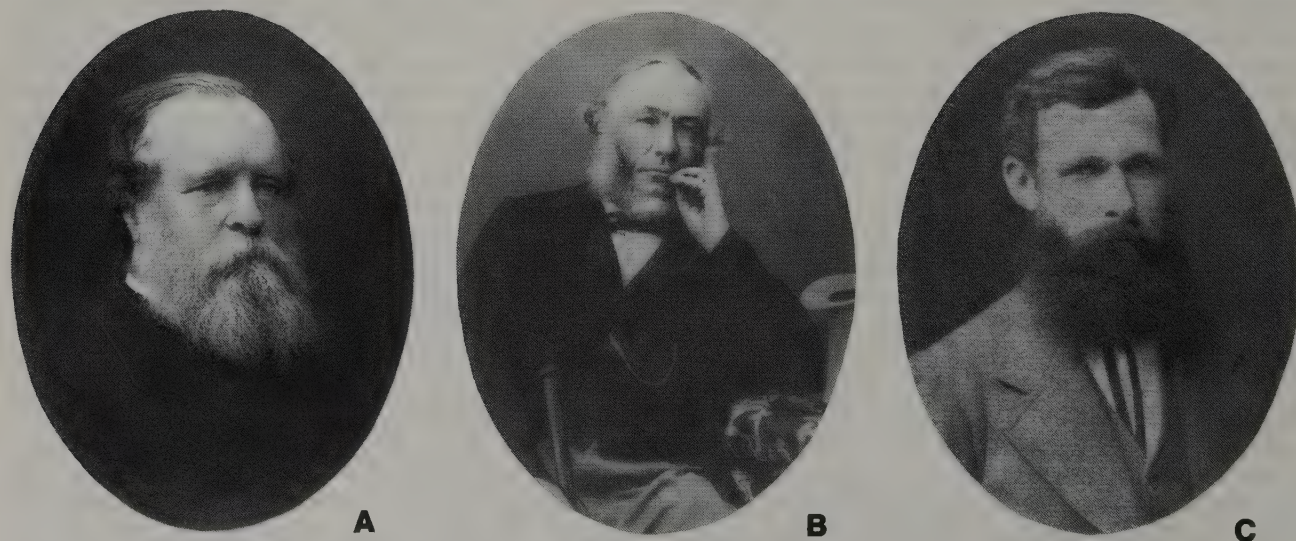


Fig. 8.2 A, William John Macleay; B, Silvester Diggles; C, George Masters.

Australia (1852–75) collecting for the Godeffroy Museum, Hamburg; about 1866 Dämel sent him another collection from Port Denison and Cape York. From the latter locality, Macleay described the giant carabid beetle *Mecynognathus dameli*.

Although at this period several women were interested in insects, including the Scott sisters, and a Mrs Kreusler of Gawler Town, S.A., who sent specimens to R. L. King, only one undertook single-handed, field expeditions. This was another Godeffroy Museum collector, Amalie Dietrich (1821–91) (L. A. Gilbert 1972) who spent 1863–71 in Australia, principally in Qld, making general collections which included insects. Daughter of a leather worker, she had been trained by her estranged husband, who preferred collecting natural history specimens to his profession of chemistry. Amalie was fearless and unconcerned with discomforts. She wrote with enthusiasm 'What freedom I enjoy here as a collector. No one circumscribes my zeal'. On return to Germany she worked for the Godeffroy and later in Hamburg's Botanical Museum.

Entomology Diversifies

As we have seen, Australian entomology during its first half century, under the dominating influence of Banks, was concerned with identification of the native fauna through collectors sending specimens to Europe for description; locally there was a beginning to life history studies.

The second half century followed a similar pattern but, under the influence of the Macleays and with the colonies founding their own museums, large collections remained in Australia and description of species by local amateur entomologists in local journals began.

In the third half century not only did this trend continue and greatly strengthen, with professional entomologists appointed to museum staffs, but entomology diversified due to increasing problems with insect pests of cultivated plants, with the spread of weeds, and with the recognition that certain diseases of man and domestic animals were insect-borne. As the human population grew, these problems became more pressing and governments, now with greater financial resources, appointed salaried entomologists to investigate them.

Insect pest problems had, of course, long since been discussed and control measures attempted. In 1820 P. P. King (Anon. 1967) immersed the *Mermaid* for several days in Sydney Cove to destroy the cockroaches that infested the ship. W. S. Macleay (1865) sent a note to the Entomological Society of N.S.W. on native, wood-boring beetles damaging introduced fruit trees (he recommended burning all infested trees), and William Macleay in the 1880s published several notes on destructive insects.

Some Entomologists in Museums, Government Departments and CSIR/CSIRO

In the 19th and early 20th centuries, men came to be professional entomologists by varied routes. Well into the twentieth century, botany and zoology were compulsory subjects in most medical schools and it will be seen that

many early naturalists discussed here had medical training.

Arthur Sidney Olliff (1865–95) (Froggatt 1912; Gibbney and Smith 1987) educated at University College, London, had been curator and private secretary to Lord Walsingham, a noted lepidopterist, before he took up appointment as Assistant in Entomology (i.e. departmental curator) at the Australian Museum in 1885. In 1890 he was appointed Government Entomologist in the newly created Agricultural Department of N.S.W. He published mainly taxonomic papers on Coleoptera and Lepidoptera and, from 1890, notes on insect pests, including codling moth. His 43-page *Australian Butterflies: A Brief Account of the Native Families with a Chapter on Collecting and Preserving Insects* (1889) which is the first popular book exclusively on Australian butterflies, began as a series of newspaper articles. His early death followed 'a protracted physical breakdown'.

Olliff was not the first Government Entomologist in the Australian colonies. This distinction belongs to Charles French Snr (1842–1933) (Pescott 1981), appointed in Vic. in 1889. French's interest in insects dated from his boyhood in England. He came to Vic. in 1852. Apprenticed to a nurseryman in 1858 he developed outstanding horticultural expertise and was appointed to the Melbourne Botanic Gardens in 1865 and to the Herbarium in 1881. About 1860 he resumed collecting insects (he made and sold three collections of Coleoptera in his lifetime), and an article by him on timber-boring insects was published in the Department of Agriculture's annual report in 1874. As Government Entomologist (1889–1908) he was concerned with spraying and fumigation programmes. He published little besides the *Handbook of Destructive Insects of Victoria* Vols I–V (1891–1911), but did much to promote interest in insects through the Field Naturalists' Club of Vic., which he helped to found in 1880. His son, Charles French Jnr (1868–1950) was later also Victorian Government Entomologist.

In the late 1880s William Macleay employed two bright young men, F. A. A. Skuse and W. W. Froggatt, who together 'spent all Saturdays and holidays collecting'.

Frederick Arthur Askew Skuse (1864–96) (C. P. Alexander 1932; Strahan 1979) son of a Church of England parson, well educated, handsome and charming, had studied entomology in the British Museum (Natural History). When, in about 1887, he arrived in Sydney seeking a job, Macleay employed him to study Australian Diptera which Macleay felt had been unduly neglected. Skuse worked hard and between 1888 and 1890 published a magnificent series of taxonomic papers. Then things went wrong. Macleay was suddenly prostrated by illness and Skuse's financial support was withdrawn. In 1890 he was appointed to succeed Olliff at the Australian Museum where he got into bad company and personally 'went to the dogs', reputedly the result of consuming the Museum's alcohol. The Museum found him 'not a very productive scientist'.

Walter Wilson Froggatt (1858–1937) (Alexander 1932; Froggatt 1934; W[alkom] 1942; Hely 1968; Watson and Gay 1983) was born in Melbourne and grew up in



Fig. 8.3 A, Walter Wilson Froggatt; B, Henry Tryon; C, Henry Hacker; D, Herbert Womersley; E, Gerald Freer Hill; F, Percy Tarlton Rayment; G, George Hudleston Hurlstone Hardy; H, Michael James Denham White.

Bendigo. His father was an architect who became interested in mining. His maternal grandfather was an adventurous Italian nobleman. Walter was a delicate child and was encouraged to develop an interest in natural history. He received his first insect collection box on his sixth birthday. As a young man, he spent a period wandering to new mineral fields in northern Qld. He sent plant specimens to Baron Ferdinand von Mueller on whose recommendation he was appointed assistant zoologist to the Geographical Society of Australasia New Guinea expedition in 1885. On his return, he collected for William Macleay in northern Qld and for almost a year in north-western Australia where he travelled with a horse and spring cart and slept in a combined tent-cum-mosquito net. On one occasion he suffered with sun fever and lay alone in the tent for eight days.

Froggatt acknowledged that Macleay helped him in every way. Given leave in 1888, he visited many museums in England and on return worked in the Macleay Museum. In 1892 he became geological collector for the Technological Museum, and was appointed entomologist in the Department of Mines and Agriculture in 1896. It was at the Technological Museum that he began to study termites 'with the intention of working out the economic

aspect of their life-history'. He described 27 new species. In 1907 he published *Australian Insects*, the first comprehensive textbook on Australian entomology. He was a prolific writer and Musgrave (1932) reported: 'He has produced more papers on Australian insects than any other worker'. These included a series on the taxonomy of Australian scale insects. Froggatt had little sympathy for attempts at biological control of pest insects. In 1923 he retired as Government Entomologist, but was Forest Entomologist to the Forestry Commission from 1923 until 1927. Like French, he popularised entomology and was a founder in 1891 of the Naturalists' Society of N.S.W.

A contemporary of Froggatt was the Yorkshire-born William Joseph Rainbow (1856–1919). Primarily an arachnologist, Rainbow was entomologist at the Australian Museum from 1895 to 1919. His popular book on Australian butterflies (Rainbow 1907) spanned the gap in the natural history literature between Olliff's modest, early butterfly book, and the seminal works of G. A. Waterhouse (p. 214).

Anthony Musgrave (1895–1959) (W[hitley] 1961) followed Rainbow as entomologist at the Australian Museum. Born in Cooktown and educated in Sydney,

Musgrave started at the Museum in 1910 as a cadet and worked as assistant to Rainbow. Succeeding Rainbow, he was Entomologist (later Curator of Entomology) from 1920 to 1959. Musgrave was an active field worker and although of a rather retiring disposition, a lively lecturer. He published taxonomic papers on Hemiptera and nycteribiid flies, and many popular articles and biographical notes. He was also a skilled photographer. However, his important and lasting contribution to Australian entomology was his meticulous and detailed bibliographic and historical work. This culminated in 1932 with publication of his *Bibliography of Australian Entomology 1775–1930 with biographical notes on authors and collectors*. Musgrave prepared a supplement to this, covering the years 1931 to 1958. Although the supplement was never published bound copies of his manuscript are held by various libraries.

Johann Gottlieb Otto Tepper (1841–1923) (Musgrave 1932), who came from Germany to Australia with his parents in 1847, was entomologist at the South Australian Museum and consulting Entomologist to the Department of Agriculture from 1888 to 1911. A school teacher, he was first appointed to the Museum in 1883 as a natural history collector. Tepper published on several orders, but principally on Orthoptera and Blattodea. His *Common Insects of South Australia* (1887, 1890), although covering only Coleoptera and Lepidoptera, was perhaps the first popular guide to Australian insects published in this country. Tepper was succeeded at the museum by A. M. Lea.

Arthur Mills Lea (1868–1932) (Matthews 1985a) was Government Entomologist of W.A. from 1895 to 1898. Born in Sydney, Lea's boyhood interest in entomology had been encouraged by W. J. Macleay and Masters, and continued as a hobby until, in 1891, he was appointed assistant to A. S. Olliff. In 1899 Lea became Government Entomologist of Tas., following E. H. Thompson who had held that position from 1891 to 1896. From 1911 to 1932 Lea was entomologist at the South Australian Museum and Consulting Entomologist to the Department of Agriculture. Lea was a big man, bluff and good natured, with an ability to arouse enthusiasm and cooperation in others, including farmers. This ability contributed to his success as an economic entomologist, and to his role as a founder of the Field Naturalists' Club of Tas. He was a protagonist of biological control and a productive taxonomist. At the Museum he could work almost full time at what had been his chief leisure interest, the collection and description of Coleoptera. Altogether he described and named 5432 species of beetles, and he was his own skilled illustrator.

Herbert Womersley (1889–1962) (Southcott 1963, 1964), who succeeded Lea at the South Australian Museum in 1933, was an Englishman whose first profession was industrial chemistry. With an interest in insects from boyhood, he took a course in microscopy that gave him skills to study primitive insect groups, especially Collembola. After the 1914–18 war he devoted his spare time to the study of apterygote insects, and became the British authority on Collembola and Protura. In 1930 he

was appointed Entomologist, Section of Pasture and Field Pests, Division of Economic Entomology, C.S.I.R. (later CSIRO) to work on two pasture pests in W.A.: a collembolan, the lucerne flea, *Sminthurus viridis*, and the red-legged earth mite, *Halotydeus destructor*. Womersley first spent five months at the British Museum (Natural History) acquiring a wide knowledge of the two families to which these pests belonged, and also of field control methods. In Australia, while his spare time was spent on systematic studies of Collembola, Womersley's field studies included the role of predatory mites in the control of *Sminthurus*. Due to the Depression, his three-year contract was not renewed; instead he obtained the South Australian Museum appointment as Entomologist (1933–54). He retired from the latter post to the specially created positions of Acarologist (1954–59) and then Honorary Acarologist (1959–62). Initially Womersley concentrated on the taxonomy of apterygote insects, with his major publication being *Primitive Insects of South Australia* (1939). After 1945 almost all his publications were on Acarina, on which he became a world authority; his most important contribution, published in 1952, was his monograph of the trombiculid mites of the Oriental and Australasian regions. He was closely involved with wildlife preservation in his state and was a Commissioner of the National Park and Wild Life Reserves; rangers of the National Parks formed a guard of honour at his funeral.

From 1901 to 1910 the W.A. Government employed George Compere (Howard 1930) as Government Entomologist. He was partly funded also by the State of California. This was a period of great enthusiasm for biological control. Compere, a Californian with orchard experience, had insufficient entomological training for his task, but worked hard and travelled very widely in search of control agents. Leslie John William Newman (1878–1938) (Jenkins 1988) was Compere's assistant, then, after Compere had left, acting head of the section, and later, from 1920 to 1938, Government Entomologist of W. A. Newman was born at Port Melbourne and educated partly at the School of Horticulture, Burnley, where he later taught. His interest in entomology was stimulated by Charles French and French's son. In 1904 Newman became horticultural inspector in the W.A. Department of Agriculture, and in 1906 took charge of the insectary to receive and propagate insects sent from abroad by Compere. As Government Entomologist Newman established several successful parasitoids and predators, and gained an international reputation for his use of chemical lures and poison baits against the Mediterranean fruit fly, *Ceratitis capitata*.

He collaborated with Womersley in some aspects of the lucerne flea investigations.

Henry Tryon (1856–1943) (C. T. White 1945; Marks 1983b; Monteith and Mather 1986), the English-born Government Entomologist of Qld from 1894 to 1925, abandoned medical studies at London Hospital to pursue natural history. He came to Qld in about 1882. From 1883 to 1893 he worked at the Qld Museum, firstly as clerical assistant (1883–84) and then as Assistant Curator

(1885–93). As the only entomologist in government employ, he was increasingly called on by the Department of Agriculture for advice on economic problems. The Museum received neither credit nor compensation for this and retrenched him in 1893; his appointment to the Department of Agriculture followed. Tryon, wiry, energetic and bearded, was a clever and versatile scientist (he was also Vegetable Pathologist, 1901–25) and a leading spirit in the formation of scientific societies. He was first Secretary of the Royal Society of Qld in 1883, first President of the short-lived Natural History Society of Qld (which had a strong entomological bias) in 1892, and a founder of the Qld Naturalists' Club in 1906. Although society councillors and institutional administrators often found him difficult and sarcastic, he was encouraging to young scientists, including his own staff. His publications included important reports on orchard, sugarcane and banana pests, and on natural enemies of prickly pear (see also under Biological control, p. 210), as well as a lengthy taxonomic paper on fruit flies (Tephritidae).

An important appointment to the Qld Museum was made in 1911 when Henry Hacker (1876–1973) (Marks and Dahms 1974; Monteith and Mather 1986) became Entomologist. He had charge of the Museum's collections until 1943, although he worked there only part-time from 1929 when he was seconded to the Department of Agriculture to build up its collection. An Englishman who started his study of entomology at the British Museum, Hacker led an adventurous, wandering life, coming to Australia in the 1890s and working as a miner on the goldfields of W.A. and northern Qld. He travelled with his belongings on a bicycle and collected mainly Coleoptera, which were sent to Australian taxonomists, including A. M. Lea. About 1910 he sold his private collection of some 6000 species of Australian Coleoptera to the Berlin Museum. By his outstanding collecting ability he greatly increased the Qld Museum's holdings of all orders, he sent specimens to specialists around the world for description, and he expanded his own interests in Hemiptera and Hymenoptera. His small number of publications and his contributions to meetings of the Entomological Society of Qld (which he helped found in 1923) reveal his wide knowledge of insect habits and life histories.

The Qld Bureau of Sugar Experiment Stations was established in 1900 to tackle problems of the expanding sugar industry. By 1911 damage by canegrubs (larvae of scarabaeid beetles) was so severe that an experienced entomologist from the U.S.A. was appointed. Alexandre Arsène Girault (1884–1941) (Dahms 1978), an American of French descent, was stationed at Gordonvale from 1911 until 1914. A graduate of Virginia Polytechnic, he had worked between 1904 and 1911 as an assistant, firstly in the U.S. Bureau of Entomology, then for the Illinois State Entomologist and University. In Illinois he developed an interest in the habits and classification of chalcidoid wasps. This was to become an unswerving devotion to which personal and family considerations, and to some extent professional duties, were subjugated.

At Gordonvale, in addition to work on cane beetles,

Girault began to study Australian chalcidoids. He arranged with Hamlyn-Harris (see p. 218) to lodge his types in the Qld Museum and to publish lengthy papers in the Museum's *Memoirs*. He returned to the U.S.A. in 1914 but in 1917 came back to Qld a frustrated and embittered man. His frustrations continued. Girault's ambition for an appointment to work full-time on the taxonomy of chalcidoid wasps was never fulfilled—simply, there were no such positions available. Materials for his studies were hard to come by; the Museum helped with microscope slides and Eland Shaw (see p. 216) lent him a microscope. In the post-war period and during the Depression funds for publication were limited. Girault described thousands of new forms, publishing in whichever journals he could. Despite a meagre and often uncertain personal income, he also published 63 papers privately and was able in them to express his frustrations; they are peppered with poetry, philosophical remarks and criticisms of colleagues.

Employment at the Gordonvale Experiment Station (1918–1919) was followed by a period of poultry farming and shopkeeping, near Brisbane, with an interlude as microscopist for the Hookworm Campaign (see p. 218). In 1923 Girault obtained a temporary appointment as an assistant entomologist in the Department of Agriculture and Stock (as an American citizen he was ineligible for permanent appointment). Henry Tryon and his successor Robert Veitch had difficulty confining Girault to economic problems. His appointment, renewed at intervals of six, twelve and eventually three months, ended in 1935. In failing health, he was reduced to labouring and unemployment benefits, but in 1936–37 he received a Commonwealth grant to complete his 2483-page manuscript synopsis of the Australian Chalcidoidea, which was never published. Girault's prodigious taxonomic legacy is marred by confusions and is notoriously difficult to interpret.

Probably the first entomologist employed by the Commonwealth Government was Gerald Freer Hill (1880–1954) (Gay 1954; Whittell 1954; Watson and Gay 1983). A gentle, kindly man and a versatile naturalist, Hill was born in Melbourne and attended Burnley Horticultural School. After fruit growing for a few years he became a shorthand instructor and moved to New Zealand. Returning to Australia in 1908, he collected bird eggs and skins in north-western Australia in 1910 and was Naturalist to the Commonwealth Government Exploration Party, Central Australia and N.T. (1911–12). From 1912 to 1917 he was Government Entomologist of the N.T. where he reported on mosquitoes and developed a great interest in termites. During 1918–19 he worked on sheep blowflies as Walter and Eliza Hall Fellow in Veterinary Research, University of Melbourne, and in 1919 he went to the Australian Institute of Tropical Medicine (AITM), Townsville, to work on mosquitoes. In 1923 he returned to Melbourne as Entomologist at the National Museum. In 1926 Hill was the first entomologist appointed by the Australian Institute of Science and Industry and, when the CSIR Division of Economic Entomology was organised in 1928, he became Assistant



Fig. 8.4 A, Robin John Tillyard; B, Alexander John Nicholson; C, André Léon Tonnoir.

Chief, a post he relinquished in 1929 to devote himself to termite research.

The Division of Economic Entomology was set up in 1928 to investigate, in a manner beyond the resources of the various State Departments of Agriculture, some of the major problems of Australian applied entomology. The first Chief of the Division was Robin John Tillyard (1881–1937) (J. W. Evans 1947, 1963b). Some others of its early staff were G. A. Waterhouse (see p. 214), I. M. Mackerras (p. 219), A. Tonnoir (below), H. Womersley and A. J. Nicholson (p. 211).

When the CSIR Executive persuaded Tillyard to become the first Chief of the Division in 1928, he was already the most influential and internationally renowned entomologist in the Australian region. He summarised his proposed research program as ‘the control of noxious weeds by their natural enemies and the control of insect pests by beneficial parasites and predators’. However he was temperamentally unsuited to be a civil servant and was essentially a systematic entomologist.

Born at Norwich, England, Tillyard took a boyhood delight in natural history. During his lifetime he won numerous prestigious awards and medals. Entering Cambridge University he graduated BA in 1903 and in 1904 he took up an appointment as a Mathematics and Science Master at Sydney Grammar School. He was an excellent teacher but an increasing interest in dragonflies (he first published on them in 1905) led him to resign in 1913 to take up a Research Scholarship at the University of Sydney. He earned a BSc by research in 1914 and a DSc in 1917 (he was awarded a Cambridge ScD in 1920). He was Linnean Macleay Fellow in Zoology between 1915 and 1920 and prepared nearly 50 publications on Odonata, including his 1917 book, *The Biology of Dragonflies*.

A visit to New Zealand in 1919 to advise on problems of trout food led to Tillyard’s appointment in 1920 as the

first Chief of the Biological Department of the Cawthron Institute, Nelson. In 1921 he introduced into New Zealand from the U.S.A. the parasitic wasp *Aphelinus mali* which quickly controlled the woolly aphid, *Eriosoma lanigerum*, a major orchard pest. While at Nelson, he wrote with the help of many colleagues *The Insects of Australia and New Zealand* (1926). This book remained the bible of Australian entomology for nearly half a century. Tillyard continued to publish on Neuroptera, Plecoptera, Ephemeroptera, Trichoptera and other orders, on wing venation, on phylogeny and on fossil insects. He was elected F.R.S. in 1925 and left New Zealand for Canberra in 1928.

Tillyard had a mercurial personality with an indomitable spirit; he was a convincing and dramatic lecturer, and wherever he travelled he took an infectious enthusiasm. His wife, Patricia, participated actively in his interests and illustrated some of his publications. His death, at 56, was the result of a motor accident.

In 1929 Tillyard recruited to the Division of Economic Entomology a former colleague from the Cawthron Institute, André Léon Tonnoir (1885–1940) (Musgrave 1932). Tonnoir, born in Brussels, Belgium, had studied in the Natural History Museum there before coming to the Cawthron in 1921. From Nelson Tonnoir went to Christchurch, first as Assistant Curator at the Canterbury Museum (1924–26), then as Lecturer in Entomology at Canterbury College (1925–26). He then returned to Nelson and the Cawthron Institute as Field Entomologist. Tonnoir was essentially a systematist, especially of Diptera. He elucidated life histories and collected widely (he died on a field trip). In Canberra he reared numerous introduced parasites for the biological control programs but his most important and lasting achievement was the firm establishment of the Division’s insect collection, initiated by G. A. Waterhouse (p. 214). In 1936 Tonnoir wrote to A. A. Girault: ‘We are gradually building up here

a fine national entomological collection which in a few decades will be no doubt the most important in Australia'. In 1962 this collection was gazetted by the Commonwealth Government as the Australian National Insect Collection.

Some Biological Control Entomologists

The first spectacular success in biological control of insect pests with which Australia was associated, concerned the introduction into North America of the Vedalia ladybird beetle, *Rodolia cardinalis*, to control cottony cushion scale, *Icerya purchasi*, which in the 1880s was threatening to destroy the Californian citrus industry. C. V. Riley, entomologist to the U.S. Department of Agriculture, heard from an amateur entomologist in S.A., Frazer S. Crawford, that the scale was not a problem there. Riley deduced that the scale had been introduced to California from Australia, where it was controlled by natural enemies, and, in 1888, sent out one of his Californian field agents, Albert Koebele. Koebele (1852–1924) (Howard 1930), born in Germany, became a U.S. citizen in 1880. Riley recruited Koebele in 1881 when he was impressed by the beautiful condition of specimens exhibited by Koebele at a meeting. Later Riley discovered that Koebele also had remarkable skills as a field man. Koebele arrived in Adelaide in 1888 and was taken into the field by Crawford and Tepper. There he found the ladybird beetle feeding on a large, female cottony cushion scale. In late 1888 and early 1889 he sent 129 beetles to California where D.W. Coquillett colonised and released them. By the end of 1889 the scale was no longer a problem. Koebele returned to Australia in 1891 on behalf of the State of California, and in 1895–96 for the Hawaiian Government, to collect parasites and predators of pest insects. He visited Australia on similar missions again in 1899–1900 and 1904–06. His skill as an entomologist contrasts with the inadequate training of G. Compere (see p. 207) and explains the latter's lack of success.

By the early 1900s prickly pear (*Opuntia* spp.) posed a major and ever-increasing problem to pastoralists in Qld and northern N.S.W. In 1912 the Qld Government appointed T. H. Johnston (see p. 212) and H. Tryon as a Travelling Commission to look for natural enemies in countries where prickly pear was naturalised. Rose Ethel Janet ('Jean') White (1877–1953) (Traill 1954; Mann 1970; Gibbney and Smith 1987; McFadyen 1988) was made Officer-in-Charge of a field station to be set up at Dulacca, Qld, for experiments into methods of destroying the prickly pear. Jean White was a research botanist from the University of Melbourne and (in 1909) the second woman in Australia to be awarded a DSc. She had a genial personality and the gift of communicating her enthusiasm to others. She arrived in Dulacca in July 1912 to a pegged out but uncleared site, commenced research in railway tents, and by November had the laboratory built.

The cochineal insect (*Dactylopius ceylonicus*), a coccid accidentally introduced from Brazil to India, had in the 1800s been deliberately introduced from India to Ceylon, where it successfully controlled the tree pear, *Opuntia*

vulgaris. From Ceylon, the Travelling Commission sent several cases of cactus infected with cochineal, which arrived in Brisbane in February 1913. The insects were reared at Dulacca by Jean White, who by November had a thriving colony. The first releases were made in May 1914 and within two to three years most stands of *O. vulgaris* had been destroyed. This was the only species of *Opuntia* attacked. This was the first example of the biological control of a weed in Australia. The 1914–18 war effort diverted resources, the Dulacca field station closed in 1916, and Jean White-Haney (as she was known after her marriage in 1914) did no further entomological work.

The common pest pear, *Opuntia inermis*, which in 1916 infested an estimated 60 million acres (24 million hectares) continued to spread. In 1920 the Commonwealth, Qld and N.S.W. Governments set up the Commonwealth Prickly Pear Board to investigate insects attacking prickly pear in North and South America, select and host-test the most promising, and collect and send stocks to Australia for large scale rearing, establishment in the field, and later mass distribution. Scientific staff were appointed and, in 1922, a laboratory was built at Sherwood, Brisbane, with a quarantine insectary. This insectary was probably the first in the world to be designed specifically for rearing insects received from overseas free of parasites and for host testing these insects. Three field stations were also established.

In late 1924 A. P. Dodd, who had been in charge of the Chinchilla Field Station, set out to undertake investigations in the U.S.A. During the North American winter he went to Uruguay and Argentina to investigate the phycitine moth *Cactoblastis cactorum*, larvae of which had been brought to Brisbane in 1914 by the Travelling Commission only to die before colonies could be established. In January 1925 Dodd collected mature larvae which he reared to adults at Buenos Aires; these moths laid 3000 eggs which he sent on prickly pear for a 10-week sea voyage to Sherwood. They arrived in May 1925 and were reared by John Mann, acting Officer-in-Charge of the station, who obtained 100 605 eggs from 1070 moths (527 females). The first field releases were made in March 1926. This one shipment and its successful establishment in the insectary led to rapid and spectacular control of *O. inermis*, and the continued recognition by Australian governments of the practicality of biological control measures.

Alan Parkhurst Dodd (1896–1981) (Monteith 1988), son of F. P. Dodd (see p. 213), was born in Brisbane and grew up in Kuranda, learning entomology as he helped his father. After boarding school at Townsville, he was appointed Assistant Entomologist with the Sugar Experiment Station at Gordonvale in 1912. Here he took up the study of minute scelionid and diapiiid wasps, initially under the tutelage of A. A. Girault. He had published 14 substantial papers on these wasps by the time he was aged 19 and continued to work on them until 1939. After army service Dodd returned to Gordonvale to work on sugarcane beetles with the American entomologist, J. F. Illingworth. In 1921 Dodd moved to the Commonwealth Prickly Pear Board as Assistant Entomologist,

rose to be Officer-in-Charge in 1925, and eventually became Director of the Biological Control Branch of the Qld Lands Department, from which he retired in 1962. He published a comprehensive report in 1940, *The Biological Campaign against Prickly Pear*.

After the 1939–45 war the rabbit pest problem was acute over the southern half of Australia (Fenner and Ratcliffe 1965). Introduction of the rabbit disease myxomatosis had been suggested as early as 1919, and myxoma virus was brought in for restricted laboratory trials in 1926 and again in the mid-1930s, when L. B. Bull showed that it could be transmitted by a stickfast flea (*Echidnophaga* sp.) and by mosquitoes. Field trials in S.A. suggested that the virus could be effective temporarily where vectors were abundant, but permission to release the virus from quarantine was refused. In 1949 CSIRO established a Wildlife Survey Section under the leadership of F. N. Ratcliffe (see below), and one of the Section's tasks was a scientific approach to rabbit control. Field trials with myxomatosis in the Murray Valley gave similar results to Bull's, with the disease remaining localised and apparently dying out (Fenner and Ratcliffe 1965). However, in December 1950, the disease flared up in widely scattered areas and a widespread epizootic followed. Spread was believed to be due to the spread of infected insects; transmission was shown to be mechanical, on an infected proboscis. Rabbit kills of over 99% occurred. Until 1955–56 Ratcliffe had a team of about six scientists working on myxomatosis in the field. Ratcliffe himself often took part in the field work. Extensive biological information was obtained on vectors, the chief of which were mosquitoes. Some of the new, vector species collected were described by N. V. Dobrotworsky (see p. 218).

Francis Noble Ratcliffe (1904–70) (Mackerras 1971a) was born in Calcutta, studied zoology at Oxford, and first came to Australia in 1929–31 to undertake an ecological-economic study of flying foxes (fruit bats). He returned in 1935 to join CSIR as scientific adviser to the Executive, and made a survey of soil erosion in the arid inland. In 1937 he transferred to the Division of Economic Entomology and took part in termite investigations. He joined the army in 1942, serving as Assistant Director of Entomology at Land Headquarters and as Malariologist in the field. He was a gentle, kindly man, always concerned with the welfare of those who worked with him. After the war he led the Wildlife Survey Section (1949–61) and then returned to the Division of Entomology as Assistant Chief. He was a key figure in bringing about the establishment of the Australian Conservation Foundation in 1964 and was its first Honorary Director. He collaborated with the virologist F. Fenner in the book *Myxomatosis* (Fenner and Ratcliffe 1965), in which Ratcliffe summarised the biological information obtained on vectors.

Some University Teachers

Until the 1920s entomology was taught in invertebrate zoology courses at Australian universities, with non-university entomologists brought in to lecture agriculture,

medical and forestry students. Froggatt, French and Lea gave lectures at the universities in their respective cities. A keen naturalist from boyhood, Launcelot Harrison (1880–1928) (Walsh 1983) was born at Wellington, N.S.W., and, after matriculating, worked in an insurance firm until he entered the University of Sydney in 1911. He won the University Medal in Zoology in 1914 and a scholarship to Cambridge. He served as an advisory entomologist to the British Expeditionary Force in Mesopotamia (1916–18), controlling insect-borne diseases, and returned to Australia in 1919 as Lecturer in Zoology at the University of Sydney. He became acting Professor in 1920 and was Professor of Zoology from 1922 to 1928. His own, principal research was on mallophagan lice and he was one of the first to recognise that the relationships of ectoparasites reflected the relationships of their bird hosts. He was also interested in the origins of the Australian fauna and an exponent of the Antarctic radiation theory, which antedated the Wegener hypothesis of continental drift. A stimulating lecturer, he was an inspiration to his students, among whom was I. M. Mackerras (see p. 219). One of his staff was Alexander John Nicholson (1895–1969) (Anon. 1970; Mackerras 1971b), the first Lecturer in Entomology appointed to the University of Sydney (1921–30) and indeed in Australia. Nicholson was born in Ireland and, as a boy in Birmingham, England, developed interests in natural history and photography. He graduated from Birmingham University in 1915 and, after war service, returned there to take his MSc with an entomological thesis. On his way to Australia he visited teaching and research institutions in the U.S.A. Determined 'not to rear students on an undiluted diet of morphology', he went on collecting trips with local amateurs to familiarise himself with the fauna and used photographs to illustrate insect habits and life histories. He put university teaching of entomology on a firm, scientific foundation, inaugurated field trips, and provided the first agricultural graduates to bring a new approach to economic entomology. His research findings (see Chapter 10) earned him a DSc from the University of Sydney.

In 1930 Nicholson left the University to become Deputy Chief of the Division of Economic Entomology of CSIR and eventually Chief (1936–60). There he planned with great care and strove for a judicious balance between fundamental and applied research. He held the Division 'unobtrusively but effectively, to the highest standards of endeavour and scientific integrity'. His studies of population dynamics and natural selection were mainly in the post-war period and continued after his retirement. He published two important papers on these subjects (1933, 1960) but died before writing up his later experiments.

In 1930 Nicholson was succeeded as Lecturer in Entomology by Anthony Reeve Woodhill (1900–65) (Pasfield 1965; Lee and Waterhouse 1968). Born at Nowra, N.S.W., Woodhill commenced the Agricultural Science course at the University of Sydney in 1920 and thus was able to attend both Froggatt's and Nicholson's courses in entomology. On graduation in 1924, he was

appointed Assistant Entomologist in the N.S.W. Department of Agriculture where he worked on orchard pests and on sheep blowflies, until returning to the University of Sydney. Thereafter his main research concerned mosquitoes—their behaviour and development; then, during war service between 1942 and 1945, anopheline taxonomy in collaboration with D. J. Lee; and, later, experimental crossing of *Aedes* (*Stegomyia*) spp. These studies earned him a doctorate in Agricultural Science and he was promoted to Reader. Woodhill was an unassuming man who earned the high regard of his students.

The Waite Agricultural Research Institute of the University of Adelaide was established in 1923. In 1928 an ecologist, James Davidson (1885–1945) (Browning 1981) arrived to head the Entomology Department and in 1937 he became the first Professor of Entomology in an Australian university. Born in Cheshire, England, Davidson was a DSc of Liverpool University and had worked on ticks with G. H. F. Nuttall. After service in the 1914–18 war he became assistant entomologist at Rothamsted, studying aphid-plant interactions. In Adelaide he developed the concept of 'bio-climatic zones' that limited the distribution of many species. He was a leader in the movement to make ecology a quantitative science.

Thomas Harvey Johnston (1881–1951) (Sandars 1954) took the position of Lecturer-in-Charge of the Department of Biology in the newly established University of Qld in 1911; he became Professor in 1919. Born in Sydney, Johnston was a brilliant and hard-working student, graduating both BSc and MA from the University of Sydney in 1907. After high school teaching and lecturing at Sydney Technical College, in 1909 he was appointed Assistant Microbiologist to J. B. Cleland who headed the newly established Bureau of Microbiology, Sydney. The scope of the Bureau and the natural history interests of Cleland were wide and together he and Johnston began to investigate and publish extensively on parasites of native fauna. Some of these parasites were received from T. L. Bancroft (see p. 217). Johnston's DSc thesis in 1911 was on cestode worms. A lucid and enthusiastic lecturer, Johnston gave his students plenty of practical work in the laboratory and in the field. In September 1912 he was appointed Chairman of the Prickly Pear Travelling Commission and with H. Tryon and Secretary C. W. Holland spent nearly two years abroad. Johnston and Tryon were known as the 'prickly pair'. Johnston was Officer-in-Charge of the Commonwealth Prickly Pear Laboratories from 1920 to early 1923, with leave of absence from his universities. (He had been appointed to the Chair of Zoology in the University of Adelaide in 1921.) He planned and guided the early researches of the Laboratories and spent part of 1920 in the field in North America. In Adelaide he continued his research on helminths. In Qld two of his young graduates, M. J. Bancroft (see p. 219) and O. W. Tiegs (see below) successively held Walter and Eliza Hall Fellowships in Economic Biology and researched potential vectors of livestock parasites. As senior co-author with each of them, Johnston published on the biology of sarcophagid,

muscoid and calliphorid flies, and described new species.

Oscar Werner Tiegs (1897–1956) (Anon. 1957; Drummond 1957) was born in Brisbane and graduated BSc with first class honours in Biology from the University of Qld in 1919. After two years as Walter and Eliza Hall Fellow, in 1922, he joined the Zoology Department in the University of Adelaide, where he obtained his DSc in 1925. Appointed a lecturer in zoology in the University of Melbourne in 1925, he won awards in 1928 which took him abroad until 1931, when he was appointed Associate Professor. In 1948 he became Professor of Zoology. Tiegs was kind and unassuming, and an excellent lecturer who preferred benchwork to administration. His researches embraced insect metamorphosis, the embryology of insects and myriapods, the structure of voluntary muscle fibres, and arthropod evolution. They earned him Fellowship of the Royal Society in 1944.

A Faculty of Agriculture was established in the University of Qld in 1926 and lectures commenced in 1927. The first Lecturer in Economic Entomology was Frederick Athol Perkins (1897–1976) (Marks 1977). Born in Sydney, Perkins graduated BAgSc from the University of Sydney in 1921, and worked in the Entomology Branch of the N.S.W. Agriculture Department until mid-1922. There he studied entomological techniques and reorganised the collections and library, a valuable foundation for his subsequent career. After the 1914–18 war soldier settlers in the Stanthorpe district of Qld encountered serious fruit fly problems, and the Qld Agriculture Department sent a senior entomologist, Hubert Jarvis, to Stanthorpe to work on orchard pests. Funded by a Government grant for additional fruit fly research, in 1922 Perkins became the University of Qld's District Research Fellow at Stanthorpe. The first aim was to discover whether the flies hibernated in the area or invaded it seasonally. Perkins and Jarvis did a great deal of field collecting. In search of hosts Perkins reared many species of tephritids and he later published extensively on their taxonomy. In the University Perkins lectured rather informally and was a friend to his students. He emphasised the importance of accurate identifications and field observations and fired students with some of his own enthusiasm. From 1952 until his retirement in 1965 Perkins was Reader-in-Charge of the first autonomous Department of Entomology in an Australian university. The first lecturer recruited to his staff, in 1952, was T. E. Woodward.

Thomas Emmanuel Woodward (1918–85) (Monteith 1986) was born in Auckland, and was one of the first graduates in entomology of the University of New Zealand. After completing his MSc he entered the army and, at war's end in 1945, took his discharge in London to undertake a PhD at Imperial College, where he studied the reproductive cycle in Hemiptera. After this stimulating period he returned to Auckland as Lecturer in Zoology for three years before moving to the University of Qld, from which he retired in 1983. In Qld his chief research interest was the systematics of lygaeid bugs. A kindly man, his energetic field collecting, broad intellectual background, deep entomological knowledge and

meticulous precision equipped him well to guide postgraduate students in systematics.

While Adelaide developed a postgraduate school in ecology and Qld one in systematics, the centre for insect genetics was at the University of Melbourne, after the appointment of M. J. D. White as Professor of Zoology. White eventually transferred to the Chair in the newly created Department of Genetics and after his retirement in 1975 he was Visiting Fellow at the Australian National University, Canberra.

Michael James Denham White (1910–83) (Key 1984) was born in London and grew up in Italy and France. He attended University College, London, and was later on the Zoology Department staff there, before moving to appointments in the U.S.A., including one as Associate Professor of Zoology at the University of Missouri. White first visited Australia in 1953. Described at his death as the world's leading cytogeneticist, he was a Fellow of the Royal Society, an inspiring lecturer and a tireless worker in laboratory and field. Collaborating fruitfully with the systematist K. H. L. Key, he opened up a whole new field of research in studies of the Australian grasshopper subfamily Morabinae and problems of parapatric speciation.

Some Collectors and Taxonomists

There has always been a great deal of insect collecting undertaken in Australia for museums and private collections located in this country and overseas. In earlier years, private collectors ('amateurs') were also heavily involved in the description of the Australian fauna, but increasingly this has become the task of professional entomologists in institutions which can provide such necessities as sophisticated microscopes and comprehensive libraries. The amateurs played (and continue to play) an invaluable role in another way. They built up fine, specialist collections, many from localities that have since been altered irrevocably. In doing so, they provided significant distribution, life history and habitat records. Fortunately, many of their collections have found their way, by gift, bequest or sale, into Australian institutions, where they can today be studied.

Rowland Illidge (1846–1929) (Tryon 1929) was born in London and arrived in Brisbane with his family in 1859. His boyhood interest in insects (and birds) was encouraged by Silvester Diggles, whose Lepidoptera collection he later acquired, and Illidge, in turn, inspired many other naturalists, among them F. P. Dodd (see below). Illidge collected mainly beetles and butterflies and published on their distribution and food plants. His beetle collection was given by his sons to the University of Qld's Entomology Department. T. P. Lucas (1891), to whom Illidge sold his butterflies, recounted how, in the late 1870s, Illidge 'climbed a eucalypt tree, 40 yards high, on the bank of the Brisbane River on what is now . . . North Quay. He succeeded in obtaining a congregation of some 40 or 50 hard woody cocoons on a large plant of mistletoe, and was fortunate to breed out a good harvest of [the] moth', *Opodiphthera loranthe*. Illidge was a school teacher between 1868 and 1876, and later an insurance writer. He enthusiastically supported natural history societies.

Thomas Pennington Lucas (1843–1917), a medical practitioner, arrived in Australia in 1876, practised in Melbourne for ten years and then settled in Brisbane. He invented a well known local remedy of the time, Dr Lucas's Pawpaw Ointment. Lucas became interested in natural history as a boy on walks with his geologist father on the English moors. He published numerous taxonomic papers on Lepidoptera and eventually sold his extensive collection (which included the collections of Illidge and Diggles) to the South Australian Museum.

In the Natural History Society of Qld, Illidge made a notable impression on Frederick Parkhurst Dodd (1861–1937) (Monteith 1988). Dodd recalled (quoted in Monteith): 'With Mr Illidge I quickly formed a close acquaintance, intuitively recognising in him a great naturalist. With him for a guide and friend, my knowledge widened, whilst my interest ever outpaced it'. Dodd was born at Stawell, Vic., and in 1879 became a bank clerk. He was transferred to Townsville in 1884 (where his interest in insect collecting was aroused by a 'fellow-lodger') and then to Brisbane in 1888. In 1895 he decided to make insects his sole means of living by supplying specimens to museums and wealthy collectors in Europe. Much of this material, including 18 000 moths sold to Lord Walsingham, is now in the British Museum (Natural History). Dodd took his family to Townsville in 1899 and moved to Kuranda in 1903. The children (including A. P.



Fig. 8.5 Frederick Parkhurst Dodd.

Dodd) all had their allotted tasks in the insect business. Later, Dodd collected at Darwin and in New Guinea. He published observations on insect habits and life histories. During the 1914–18 war Dodd developed a display collection for exhibit to tourists. In 1918 and again in 1923 he toured southern states with his collection rousing the interest of many young people in entomology. The surviving 40 cases of insects from this travelling collection were given by his descendants to the Qld Museum in 1987.

Some 2300 Australian microlepidoptera and about 500 Australian macrolepidoptera (excluding synonyms) were named by Edward Meyrick (1854–1938) (Common 1983), a Cambridge BA, who arrived in Sydney in 1877 to teach classics at Sydney Grammar School. After spending 1882 in New Zealand, he taught at King's School Parramatta from 1883 to 1886, before returning to England. Meyrick was fascinated by the rich fauna of microlepidoptera which he found in New South Wales in the Sydney area and on later trips to the other Australian colonies. He set himself rigid, scientific standards for his taxonomic descriptions but seldom designated type specimens. In a series of lengthy papers he established classifications for many moth families and, after he returned to England, he became the world authority on the microlepidoptera. His private collection passed to the British Museum (Natural History) after his death.

Meyrick had a great influence on Alfred Jefferis Turner (1861–1947) (Mackerras 1949; Common 1983; Thearle 1986). Turner, the son of an English missionary, was born in Canton, China, and graduated MD from the University of London in 1886. He came to Australia in 1888 and to Brisbane in 1889 where he became a distinguished pediatrician and microbiologist, a crusader on matters of public health, and, at the age of 65, Qld's first Director of Infant Welfare, a post he held for 12 years. In appearance rather a frail, gentle person, with quiet charm, he also displayed wit, enthusiasm and clarity of mind. In his taxonomic work he followed the precepts laid down by Meyrick, but unlike Meyrick, Turner mostly designated type specimens. Today about 3600 valid specific names are attributable to Turner. He travelled widely in Australia

and was an energetic collector, as evidenced by his climbing a city railway station lamp post to capture a rare moth, behaviour that caused quite a crowd to gather. In 1932 he arranged with Tillyard, whom he had helped in the preparation of *The Insects of Australia and New Zealand*, that on his death his collection of 55 000 specimens (including many primary types) would pass to CSIR. In its turn, CSIR provided Turner with cabinets for the collection, which went to Canberra in 1947.

Common (1983) has called the period from about 1870 to 1940 the Meyrick-Turner period in the history of Australian Lepidoptera. In these years there was prolific genus and species description, usually based on relatively few, superficial characters of adults. After the 1939–45 war great advances in knowledge of the biology and morphology of Lepidoptera inevitably led to revision of Meyrick's classifications.

Another prolific Lepidoptera taxonomist from the Meyrick-Turner period was Oswald Bertram Lower (1863–1925) (Common 1983) who was born in Adelaide and worked there and in Broken Hill as a pharmacist. He was responsible for about 800 valid Lepidoptera names and his collection went to the South Australian Museum.

Gustavus Athol Waterhouse (1877–1950) (Walkom and Nicholson 1954; Common and Waterhouse 1981), who alone or in collaboration with G. Lyell or R. E. Turner named 15 (presently valid) genera, 29 species and 118 subspecies of Australian butterflies, had a more experimental approach to systematics than the lepidopterists mentioned above. Born in Sydney, Waterhouse grew up in an atmosphere of natural history. He began collecting butterflies at age 16 and published his first papers on them in 1897. He graduated from the University of Sydney BSc with first class honours in Geology in 1899 and BE in 1900. By contrast he obtained his DSc in 1924 for a thesis based on his work on hybridisation in butterflies of the genus *Tisiphone*. Waterhouse was Assistant Assayer at the Sydney branch of the Royal Mint from 1900 to 1926 when the branch closed. In 1928 he joined the newly formed Division of Economic Entomology of CSIR as one of its first officers, with the title of Curator and

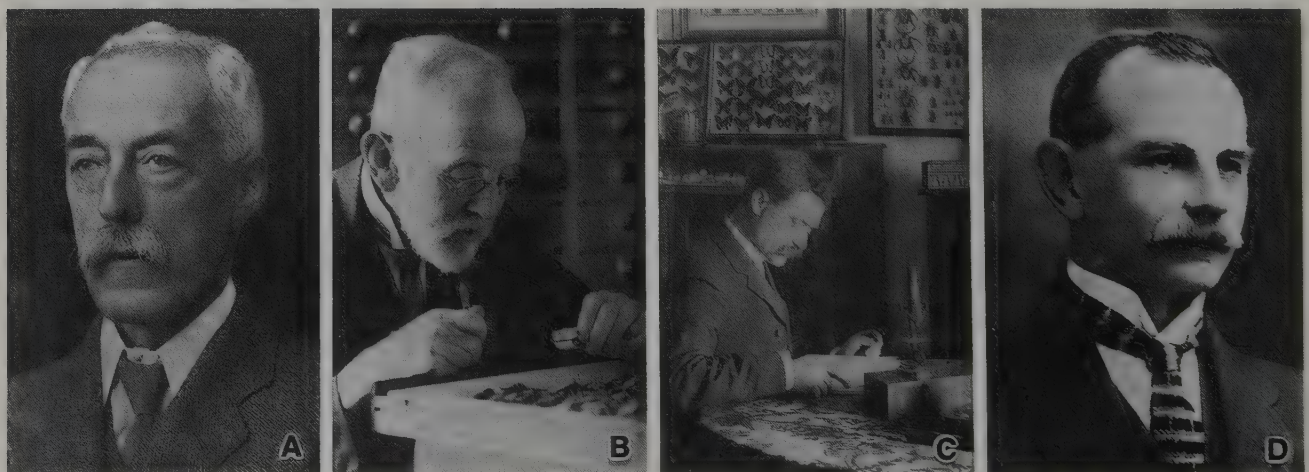


Fig. 8.6 A, Edward Meyrick; B, Alfred Jefferis Turner; C, Oswald Bertram Lower; D, Gustavus Athol Waterhouse.

Administrative Officer, and the task of organising buildings and equipment and initiating an insect collection. He resigned from CSIR in 1930 and presented his extensive, private collection of over 50 000 specimens to the Australian Museum. Waterhouse gave long service in the administration of scientific and natural history societies. In 1921 he initiated an Entomological Section of the Royal Zoological Society of N.S.W. (Marks and Mackerras 1972). Its members spent collecting weekends at the Society's cottage in the (Royal) National Park, where the young I. M. and M. J. Mackerras and A. J. Nicholson absorbed entomological lore from Waterhouse and his contemporaries (Mackerras 1971b; Mackerras and Marks 1973). Waterhouse's major publication was *The Butterflies of Australia* (1914), prepared in collaboration with Lyell (see below). This book 'remains the only comprehensive, fully documented work on the Australian butterfly fauna' (Common and Waterhouse 1981, p. 3). Waterhouse's more widely available, popular book *What Butterfly is That?* (1932) was an even greater stimulus to naturalists. Waterhouse himself was infectiously enthusiastic, kindly and helpful, and he influenced a number of other collectors to leave their insects to museums.

George Lyell (1866–1951) (Neboiss 1986b), co-author with Waterhouse of *The Butterflies of Australia*, built up an enormous collection of moths (some 45 000 specimens) which in 1932 he gave to the Museum of Vic. (known at the time as the National Museum of Vic.). Lyell, who was born at Ararat, Vic., became interested in insect collecting in 1888 and joined the Field Naturalists' Club of Vic. whose members included Charles French Snr. For much of his life, Lyell worked as a partner in an East Gippsland firm which manufactured appliances for butter factories and dairies. No doubt it was Lyell's influence that resulted in the firm branching out into manufacturing and selling entomological supplies.

Coleoptera vie with Lepidoptera as the most popular group among amateur insect collectors.

Prominent among the early Australian, amateur beetle collectors was the quiet and unassuming Rev. Canon Thomas Blackburn (1844–1912) (Lea 1912; Blackburn

1979). Blackburn was born in Liverpool and interested in entomology from an early age. While still a teenager he and his brother co-edited and published *The Weekly Entomologist*, a serial which ran for two years before giving place to the *Entomologists' Monthly Magazine*. Blackburn entered the Church of England, spent six years in Hawaii, where he found time for entomology, and was then posted to S.A., first to Port Lincoln (1882) and finally to Woodville, near Adelaide (1886). Always busy with parish duties, he was often unable to commence work on his beetles until after 9pm, but he still managed to produce over 3000 printed pages on Australian Coleoptera. He worked on specimens he had collected himself, especially in S.A., and material received from many collectors, expeditions and institutions. He covered many families, including some of the most difficult groups, but evidenced little interest in the life histories of the insects themselves. He sent many of his primary types to the British Museum (Natural History) but the bulk of the material upon which he worked is in Australian institutions, especially the S.A. Museum.

Herbert James Carter (1858–1940) (Carter 1933; W[alkom] 1943; I. M. Mackerras 1949; Franki 1979), also born in England, obtained his Cambridge BA in 1881 and in 1882 was appointed assistant mathematics master at Sydney Grammar School. He became Principal of the Ascham Girls School (1902–14) and, later, an Editor of *Australian Encyclopaedia* (first published in 1927). His interest in entomology was kindled by his schoolboy sons and their friends, and encouraged by George Masters. Carter recorded many of his field experiences in his book *Gulliver in the Bush* (1933), which gives a lively picture of the entomological community at that time. The first of his 65 papers was published when he was aged 47, and alone, or jointly with E. H. Zeck, he described 55 genera and 1234 species of Coleoptera. I. M. Mackerras (1949) described Carter: 'Tall, grey, bearded, he was an indefatigable collector with umbrella and net, and a sheer delight to all who accompanied him'. Carter frequently collected on horseback and wrote in his book: 'Gradually my horses became adapted to the collecting methods, learning to

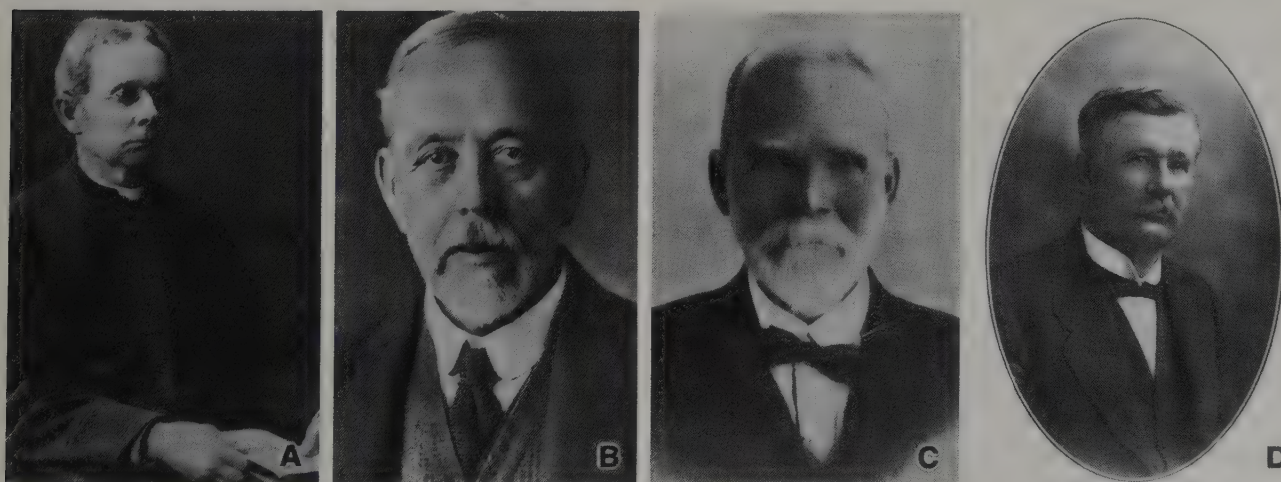


Fig. 8.7 A, Thomas Blackburn; B, Herbert James Carter; C, Thomas Gibson Sloane; D, Arthur Mills Lea.

force their way through the scrub, and stand at ease when I reached over the higher branches—even after some time learned to stop at a flowering bush—like some bushmen's horses do at the pubs'.

Thomas Gibson Sloane (1858–1932) (I. M. Mackerras 1949; Moore 1985), born in Melbourne, became a pastoralist in southern N.S.W. As a young man he knew William Macleay who perhaps inspired his interest in beetles. He collected widely in Australia and, between 1881 and 1923, published 61 papers, chiefly on Carabidae (he described about 550 species). His collection deteriorated badly before reaching CSIR to whom he had bequeathed it.

Among the many collectors who visited Australia for extended periods, Philip Jackson Darlington, Jnr (1904–83) (Carpenter 1985; Moore 1985), deserves special mention. An American carabid specialist based at Harvard University, he first came to Australia in 1931–32 with the Harvard Expedition and collected widely under the leadership of the ant specialist W.M. Wheeler. During 1956–58 Darlington returned to Australia to spend 14 months collecting Carabidae in 'practically every important piece of wet forest from the northern tip of Cape York to the southern tip of Tasmania'. The series of papers resulting from this fieldwork and Darlington's wartime collecting in New Guinea, drew the attention of Australian entomologists to their unique rainforest fauna.

Other expeditions by foreign collectors include the Hamburg South-Western Australian Research Expedition of 1905, led by Wilhelm Michaelsen (1860–1937) and R. Hartmeyer. The Expedition collected most orders of insects, specimens were sent to specialists for identification and description, and resulting papers were published in 1920 in an impressive work *Die Fauna Sudwest Australiens*. Swedish Scientific Expeditions to north-western Australia during 1910–11 and Qld during 1912–13 were under the leadership of Eric Georg Mjöberg (b. 1882). Both the Swedish and the Hamburg expeditions made particularly significant contributions to knowledge of Australian termites (Watson and Gay 1983).

Cockroaches were the specialty of Alfred Eland Shaw (1861–1931) (Gibbney and Smith 1987). Shaw was born in Ireland and worked at the British Museum for some time before graduating in medicine in 1892. He had been publishing on British orthopteroids for several years before coming to Australia in 1910. He practised medicine first in Healesville, Vic., then successively in New Guinea, the Brisbane area and Sydney. While living in Wynnum, a bayside suburb of Brisbane, Shaw lent a microscope to the impecunious A. A. Girault, who at the time had a fruit and vegetable shop in the same suburb. Between 1914 and 1925 Shaw published six papers on Australian cockroaches. His collection was purchased by the Qld Museum.

Over 1000 Australian insects, mainly bees and wasps, were described by Percy Tarlton Rayment (1882–1964) (Young 1967; K. L. Walker 1988). Born in Reading, England, and trained as an artist, he came to Vic. in 1902, and practised as a commercial artist in Ballarat. He was a shortish man with a ruddy complexion, fair hair and penetrating blue eyes. Fascinated with bees since childhood,

he decided to take up beekeeping, first at Leongatha and then, from about 1908, at Briagalong, where he had 300 hives. In 1922 he moved to Sandringham, a suburb of Melbourne where the heaths were then a naturalist's paradise. For a period he was a partner in a Business College. He was a prolific writer, producing books and many articles on beekeeping, children's books, short stories, a novel, poetry and natural history articles. He became a popular radio broadcaster and helped produce two films on native bees. Inspired by J. H. Fabre and encouraged by T. D. A. Cockerell, Rayment studied native bees and their habits, drawing, dissecting and describing them, and publishing many short articles. Reviewers of his 752-page, illustrated book *A Cluster of Bees. A Monograph of the native bees of Australia* (1935) likened him to Fabre. Although capable of writing a formal description of a new species, Rayment preferred to entangle morphological notes and observations on the insect's biology in a veritable web of words. Later editors rejected lengthy manuscripts as whimsical and many descriptions of new species were never published. His collection went to CSIRO in 1960. It was appropriate that when Rayment suffered a stroke in 1956, he was treated with Royal Jelly, Australian beekeepers having responded generously to an appeal. He made a good recovery.

George Hudleston Hurlstone Hardy (1882–1966) (Hardy 1965; Chadwick 1967; I. M. Mackerras 1967), a productive dipterist, was born at Twickenham, England. Introduced to entomology in childhood by his father, he was not allowed to develop it as his profession, but instead studied engineering. In 1911 he arrived in Perth, W.A., where he found L. J. Newman was the only entomologist. Hardy worked as an electrical contractor. He started to build up his knowledge of the insect fauna by collecting and by spending spare time at the W.A. Museum, adding to and identifying its collection. This led to his appointment as Assistant Curator of the Tasmanian Museum, Hobart (1913–17). While there he was an active member of the Tasmanian Field Naturalists' Club and published his first papers on Australian insects (he used only two initials, G. H., as an author). There followed four years of study at the University of Sydney before he went to the University of Qld as a research fellow working on sheep blowfly problems. During 1935–36 he investigated insects feeding on galvanised burr at Goondiwindi, Qld, for the Prickly Pear Board, and in 1941 he returned to the University of Qld as Scientific Assistant to the then Professor of Biology, E. J. Goddard. A tall, thin man with beard and moustache—later moustache only—Hardy was quiet but persistent. He was a great supporter of scientific societies. Coming from Perth to Hobart, then Sydney, with visits to Adelaide and Melbourne, he met the local entomologists and wondered why there was no Australian entomological society. In Qld he found more professional entomologists than in all of the rest of Australia. In March 1923, a meeting at Hardy's Brisbane home decided to form a local society (which became the Entomological Society of Qld) with formation of an Australian society one of its chief objectives (Marks and Mackerras 1972). Hardy, as treasurer,



Fig. 8.8 A, Thomas Lane Bancroft; B, Lance Evon Cooling; C, Ronald Hamlyn-Harris; D, Nikolai V. Dobrotworsky; E, Ian Murray Mackerras; F, Mabel Josephine Mackerras.

provided ideas but attributed the Society's success to the work of the president, the entrepreneurial Goddard, and the secretary, J. L. Froggatt (son of W. W. Froggatt), an agricultural entomologist. Hardy retired to Katoomba, N.S.W., and in December 1952 was one of a meeting of eight people who resolved to form a society which is now the Entomological Society of N.S.W. He lived to see the formation of an Australia-wide entomological society, the Australian Entomological Society, in 1965.

Medical and Veterinary Entomologists

In China in 1877 Patrick Manson showed that a mosquito (*Culex quinquefasciatus*) was able to take up microfilariae from the blood of humans suffering from filariasis, and that these microfilariae developed further in the mosquito. This was the first real evidence that a pathogen of man underwent obligatory development in an insect and marked the birth of medical entomology (Service

1978). Microfilariae are the pre-larval stages of parasitic nematodes (filariae), and it was a Brisbane doctor and experimental biologist, Joseph Bancroft, who in 1876 discovered the adult worm which had given rise to Manson's microfilariae. The nematode was named *Wuchereria bancrofti*, after Joseph, and the story of its life cycle was eventually completed by Joseph's son, Thomas. Histories of Australian research on mosquitoes (Lee *et al.* 1980) and filariasis (Boreham and Marks 1986) have been used to compile this section.

Thomas Lane Bancroft (1860–1933) (Mackerras and Marks 1973) arrived in Brisbane from England with his parents in 1864. As a child, helping his father, he developed wide natural history interests. He graduated in medicine from the University of Edinburgh in 1883. From 1894 to 1904 he lived at Deception Bay, near Brisbane, where he had inherited his father's meatworks and experimental farm, and where he had leisure for research. At

that time it was thought that mosquitoes lived for a maximum of seven days and fed only once, and that man was infected with filariae via water in which infected mosquitoes had oviposited or died. Bancroft kept *Culex quinquefasciatus* alive for two months by feeding them on ripe bananas. In 1899, encouraged by Manson, he fed mosquitoes on a patient whose blood contained microfilariae, and showed that the filariae developed in the mosquito's thoracic muscles, becoming mature larvae in 16–17 days. These mature larvae died if immersed in water for 3–4 hours, leading Bancroft to suggest that they might enter the human host while the mosquito was biting. Experimenting in 1904 with another nematode, *Dirofilaria immitis* (the dog heart-worm), and using mosquitoes taken in the act of biting, he showed conclusively that the infective filariae escape from the tip of the mosquito's labella. In 1905 Bancroft implicated the day-biting mosquito *Aedes aegypti* in the transmission of dengue fever, but proof of this species as a vector was not obtained until 1916 by J. B. Cleland and colleagues in Sydney.

Bancroft sent mosquitoes, many of them reared from larvae, to F. V. Theobald at the British Museum (Natural History). In 1908 Bancroft published a *List of the mosquitoes of Queensland* . . ., using Theobald's descriptions and his own notes on their biology. While Government Medical Officer at Eidsvold (1910–30) Bancroft found time to collect mosquitoes and tabanid flies for F. H. Taylor (see below), breed tephritid flies from native fruits for Tryon, and collect butterflies for G. A. Waterhouse.

Mosquito life histories also interested William Robert Colledge (1841–1928) (Anon. 1928) who was an English-born Brisbane pharmacist, a keen microscopist, and a student of pond-life. In 1911, when describing the life history stages of the container-breeding mosquito *Toxorhynchites speciosus*, he was the first to suggest that predacious larvae of species of *Toxorhynchites* might be used for mosquito control.

In the early 1900s arthropod-borne diseases were of great concern to governments in Australia. Filariasis, malaria and dengue were prevalent in northern regions; there was a fear that the opening of the Panama Canal (completed in 1914) might bring yellow fever to the Pacific area; and with the withdrawal of islander labour from the Qld sugar plantations, it was once again questioned whether Europeans could undertake hard labour in the tropics and remain in complete health (Cilento 1962). In 1910 the Australian Institute of Tropical Medicine (AITM), the first medical research institution in Australia, opened in Townsville. It was funded jointly by the Commonwealth and State governments and F. H. Taylor (see below) was its first entomologist (from 1911).

In Queensland, in anticipation of a new Health Act (1911) a young Brisbane-born Health Inspector, Lance Evon Cooling (1893–1924) (Bryan 1925) did a special course in mosquito identification with the Government Entomologist, Tryon. In 1912 Cooling was put in charge of a mosquito survey of Brisbane suburbs. He experimented with larvicides and native fish as predators of

mosquito larvae, and conducted a mosquito destruction campaign. After war service he returned to mosquito work and joined the Australian Hookworm Campaign, which was a joint Commonwealth, State and Rockefeller undertaking. The Hookworm Campaign took Cooling to W.A. and the N.T. on hookworm, malaria, filariasis and mosquito surveys. In 1922 he joined the AITM, first as an assistant, and then as an entomologist, succeeding G. F. Hill. Cooling published guides to mosquito identification and biological notes, but died very young. His death has been attributed to Australian X-disease (now equated with mosquito-borne Australian encephalitis).

Another involved with the Hookworm Campaign was Ronald Hamlyn-Harris (1874–1953) (Marks 1983c). Hamlyn-Harris was born in England where he trained in estate management and bee-keeping before earning a DSc in zoology from Tübingen University, Germany. From 1903 he taught science in Qld at Toowoomba Grammar School, and in 1910 he was appointed Director of the Qld Museum, to which he recruited Hacker. Ill health forced Hamlyn-Harris to resign from the Museum and he spent 1917–21 as an orchardist at Stanthorpe, Qld. He returned to Brisbane in 1922 to take charge of the Australian Hookworm Campaign central laboratory. In 1925 the Brisbane City Council determined on a mosquito destruction campaign and in 1926 (a dengue epidemic year) appointed Hamlyn-Harris as Australia's first and only City Entomologist. He organised laboratory and field teams, investigated mosquito life histories, advised on engineering measures to reduce mosquito problems, and undertook an intensive educational campaign. Largely as a result of these efforts, filariasis had almost disappeared from Brisbane by 1934 (Marks 1982), and dengue did not recur after 1926. After the post of City Entomologist was abolished Hamlyn-Harris concluded his career lecturing in zoology at the University of Qld.

Frank Henry Taylor (1886–1945), born at Lakemba, N.S.W., worked at the AITM for two periods, 1911–19 and 1924–30. In 1930 the AITM was absorbed into the School of Public Health and Tropical Medicine (SPHTM), a joint undertaking by the Commonwealth Government and the University of Sydney, and Taylor went to the SPHTM to lecture in zoology. Taylor travelled widely on mosquito surveys, visiting the N.T., Torres Strait islands and the Murray Valley irrigation area. He published numerous taxonomic papers on Culicidae, Tabanidae, Ceratopogonidae and Simuliidae, and was the acknowledged Australian authority on Culicidae up until the 1939–45 war.

In 1951 several severe cases of human encephalitis were reported from the Murray Valley and the virus responsible was shown to be related to the Japanese B and St Louis encephalitis viruses, both of which were known to be mosquito-borne. At the same time the introduced myxomatosis virus was spreading rapidly through rabbits in the area and flying insects were thought to be the vectors. It became obvious that insufficient was known about Victorian mosquitoes and Nikolai V. Dobrotworsky (1903–81) (Colless, pers. comm.) emerged from the scientific wilderness to meet the challenge.

Dobrotworsky had been a professional entomologist in the U.S.S.R. where he had worked both as a museum taxonomist and (after a communist purge) in an agricultural experiment station. From 1940, for ten years, he survived war, German labour camps and Allied camps for 'displaced persons', eventually to arrive impoverished in Australia. O. W. Tiegs, then Professor of Zoology in the University of Melbourne, recognised Dobrotworsky's training and ability and in 1951 found for him a CSIRO-funded fellowship. This and miscellaneous grants over the next 23 years supported patient and perceptive studies of mosquito taxonomy and biology (e.g. see Dobrotworsky 1965) and later, pioneering work on the taxonomy of tipulid flies.

Medical and veterinary entomology were the fields of one of the most productive and distinguished husband and wife teams in Australian science, Ian Murray Mackerras (1898–1980) (Marks 1980b; Norris 1981) and Mabel Josephine Mackerras née Bancroft (1896–1971) (I. M. Mackerras and Marks 1973), referred to below as Ian and Jo. As 'medical zoologists' they investigated problems involving bacteria, haematozoa and helminths and associated vertebrates, as well as insects so that their contribution to Australian science goes far beyond the entomological researches outlined here.

Jo, born at Deception Bay, Qld, graduated BSc at the University of Queensland in 1918, then worked there for two years under Harvey Johnston's direction. She published with Johnston on life histories of muscoid and tabanid flies and the possible role of these flies as transmitters of livestock diseases. In 1920 she entered the medical course at the University of Sydney where she met Ian; they married on graduation in 1924.

Ian was born at Balclutha, New Zealand, and grew up in Sydney. He advanced his age to join the A.I.F. in 1915 and on discharge in 1919 entered medical and science courses in the University of Sydney. After graduating in 1924, he began research on Diptera (including mosquitoes and nemestrinids) in the Zoology Department of the University of Sydney where he was stimulated by L. Harrison and A. J. Nicholson. He and Jo came to know well the Sydney group of amateurs that included G. A. Waterhouse and H. J. Carter. After a short period with the N.S.W. Bureau of Microbiology (1927–28), Ian joined (in December 1928) the newly established CSIR Division of Economic Entomology. His task was to develop and direct a program of research in veterinary entomology. In 1930, Jo returned to entomology as an Assistant Entomologist in the same Division.

The Mackerrases were approachable and friendly and always ready to help and encourage other scientists. Ian was a solidly built man of middle height, with great mental and physical energy, infectious enthusiasm, and a wide grasp of zoology and medicine. Jo, a good, all-round naturalist, was slim and gentle, with a quiet sense of humour. Their joint researches were carefully planned and Jo could be depended upon to keep projects steadily progressing while Ian's administrative roles kept him on the move. Both took an active role in the research and in the writing up of results.

For CSIR Ian travelled widely in Australia and to the East Indies (now Indonesia) to organise his team's research on buffalo fly and attempts at its biological control by the introduction of Javanese parasitoids. He published on the taxonomy of buffalo fly and on that of flies associated with it in dung. In Australia, the blowfly research team (which included Jo and, for a time, A. J. Nicholson) demonstrated the crucial importance of *Lucilia cuprina* as an initiator of blowfly strike, studied the physiology, toxicology and behaviour of blowflies, and showed that some methods of control then in use were ineffective or uneconomical. A widespread epizootic of ephemeral fever in cattle in 1936 led Ian and Jo, together with F. M. Burnet of the Walter and Eliza Hall Institute, Melbourne, to investigate transmission of the disease: stable flies and mosquitoes were eliminated as possible vectors and they suggested that ceratopogonids (which were unavailable for testing at the time) might be agents of transmission. Later work proved this to be so.

On the outbreak of the 1939–45 war, Ian re-joined the A.I.F. and served as a pathologist in North Africa. When war reached New Guinea in 1942, malaria, dengue and scrub typhus became of prime importance. Ian was appointed Director of Entomology at Land Headquarters (LHQ) with F. N. Ratcliffe as his Assistant-Director. By his arguments and organisation, Ian played a major role in protecting the Australian armed forces from arthropod-borne diseases. By contrast, the Japanese neglected prophylactic measures. In 1943 the LHQ Medical Research Unit was set up in Cairns, in northern Qld. Jo, who had enlisted in 1942, was transferred to the Unit and was responsible for breeding and maintaining stocks of malaria-infected mosquitoes and using them to infect army volunteers.

In 1946 Ian and Jo returned to CSIR and moved to Brisbane where Ian took charge of the Indooroopilly laboratory which was chiefly concerned with cattle tick. In 1947 Ian was appointed Director of the newly established Qld Institute of Medical Research (QIMR) and Jo was appointed its Senior Parasitologist. The first task was to investigate a severe epidemic of *Salmonella* gastroenteritis in infants. Jo discovered that domestic cockroaches were minor reservoirs of infection. Most of Jo's work at QIMR was parasitological but she did work with Ian on the taxonomy and life histories of simuliid flies. Meanwhile Ian began major work on the taxonomy and biogeography of tabanids. They both took part in large-scale collecting of mosquitoes for arbovirus research.

Ian and Jo retired from QIMR in 1961 and moved back to Canberra as Research Fellows in CSIRO Division of Entomology. Jo worked thereafter on cockroach taxonomy and contributed the chapter on Blattodea to the 1st edition of the textbook *The Insects of Australia*. Ian brought his scholarship and broad experience to bear in editing this new, multi-authored textbook, which was to replace Tillyard's long-out-of-print book. Because he disagreed with certain statements by some of the contributing authors, he refused to have his name on the book as editor when it was published in 1970. Until his retirement in 1974 he continued to work on tabanids, historical and

biographical articles and the 1974 *Supplement* to *The Insects of Australia*. He played an active role in many scientific societies and was a key figure in the formation of the Australian Entomological Society (Marks and Mackerras 1972).

Conclusion

In a biographical chapter such as this it has been possible only to touch upon the complex interactions between per-

sonalities, scientific ideas, local institutions and societies, and changing social and economic conditions. Much more remains to be written about what, at different times, Australian entomologists were seeing, reading and hearing, and about how this information, or lack of it, influenced what they did and wrote. Some scientific issues and their developments in Australia are taken up in the following chapters (Chapters 9 and 10) but many others await full exploration in a definitive history of Australian entomology.

Insects and Humans in Australia

D. F. WATERHOUSE

In 1770, after accompanying James Cook in his exploration of the east coast of Australia, Joseph Banks attempted some generalisations about the natural history of the newly-discovered coast. In his journal he wrote: 'Of insects there were but few sorts and among them only the ants were troublesome to us'. He did not realise that his few landings had been made during the unfavourable winter period. During the two centuries following the first settlement in 1788, entomological studies have indicated that there are probably well over 100 000 species of native insects in Australia. For a continent with about 6% of the ice-free land area of the globe, this is a fairly generous share of an insect fauna thought to total more than ten million species. The native species, together with a sprinkling of unwelcome migrants that have gained access since European colonisation and a few beneficial ones introduced for biological control, interact with humans much as insects do elsewhere in the world. On the debit side some are nuisances, some bite or sting or cause allergies, some transmit diseases of humans, domestic animals or plants, and some damage crops, forests, timber and livestock. However, on the credit side, a large number contribute to biological control of pests, pollination of many cultivated plants, recycling of nutrients, and many other activities crucial to the perpetuation of balanced, natural systems. It is well to remember also that, of the vast assemblage of insects, no more than 10 000 or so species adversely affect humans throughout the world, although that impact is, of course, considerable.

As one measure of the importance attached to insects, by the mid-1980s there were in Australia upwards of 1000 professional entomologists engaged in research,

extension, administration and teaching—these in the employ of governmental instrumentalities, universities and other higher education authorities, museums and industrial organisations, together with a generous fringe of retired but still active professionals. There were also a goodly number of amateurs, popular writers, dealers, exterminators and pesticide vendors.

Probably only between one half and two-thirds of Australia's native insects have yet been named. In fact, the group has fared poorly in comparison with the meagre 2000 or so species of terrestrial and freshwater vertebrates. This is understandable in view of the vast numbers of insects involved, but it is also regrettable for it results in difficulties in attributing information that has been gathered to named species. While expressing hope for more rapid progress on this front, it is also necessary to stress the importance of using standardised popular names for common, striking or important insects. More than a thousand of these have been recommended after careful evaluation (Carne 1987), and these should be used whenever possible.

ARRIVAL OF HUMANS IN AUSTRALIA

Human occupation of Australia began when the first Aborigines arrived from far away to the north-west some time before 40 000 years ago. During this period the accumulation of ice at the poles resulting from the most recent ice age had lowered the ocean by as much as 100 m below its present level. This resulted in the emergence of extensive land bridges, not only between New Guinea, mainland Australia and Tasmania, but also con-

necting many islands now lying between New Guinea and Asia. Nevertheless, even at the time of lowest sea level, the shortest distance across the ocean deeps between Malaysia and Australia still involved eight sea voyages, the longest of these being nearly 70 km. These first people had, of course, been preceded by many northern organisms that had been steadily extending their ranges southwards over roughly the same route for the previous three or four million years.

In the new land the Aborigines would have recognised examples of the flora and fauna with which they had already become familiar during their wanderings through the island arcs to the north. However, as they progressed southwards, this biota became attenuated, and increasingly they encountered an extensive group of southern organisms that had evolved on the continent during the 50 or so million years of its isolation from other large land masses. No doubt many of these organisms were then as strange to them as they were to Europeans when they arrived tens of thousands of years later.

INSECTS AND ABORIGINES

Fellow Travellers

Probably the only insects to travel with the early Aborigines were human lice. These feature in dreamtime legends of Lake Macquarie (N.S.W.) and Arnhem Land (N.T.). Aborigines and thus must presumably have long antedated the arrival of Europeans. Furthermore, Bayly (1777) wrote of Tasmanian Aborigines at Adventure Bay (who at that stage had no known contact with Europeans) that they 'have many lice sticking about the neck and other parts of the body'. It is interesting however, that in 1770, Banks remarked that the mainland Aborigines (at Botany Bay and more particularly at Endeavour R.) 'seem to be intirely free from Lice' (Beaglehole 1962). The Maoris carried lice before the arrival of Europeans and lousiness may indeed have been a universal human condition, since lice have been recovered from mummies of ancient Egypt, pre-Columbian America, 15th century western Greenland and the Aleutian Is (Southcott 1986).

There is no evidence from legends that human fleas were fellow travellers but this is not surprising. Because their larval life cycle is spent off their host, fleas would have had extreme difficulty in surviving a long trek to Australia unless a fairly uninterrupted flow of people made the journey. Nakedness would not help fleas either and it is of interest that the dingo which, with its more hospitable, hairy body would be capable of transporting human-infesting fleas, did not arrive in Australia before about 4000 years ago.

Medicinal Uses of Insects

For the early arrivals in Australia, insects came to have a range of medicinal uses, although there is room for doubt as to the efficacy of these remedies in terms of modern medical practice. It is recorded that the Aborigines squeezed out the body contents of certain large moth or beetle larvae, and applied the empty cuticle to sores, wounds and burns. Sometimes affected areas were rubbed

with live cicadas and burns were treated with the squashed body contents of *Apiomorpha* spp. (HEMI: Eriococcidae) removed from their galls on eucalypts.

In some places the contents of ant pupae were regarded as a valuable treatment for head sores and winged ants, cooked on hot stones, were rubbed together in the hands and applied to sores. Sniffing the vapour of roasting ants was considered beneficial for respiratory complaints and green tree ants crushed in water were used for digestive problems. Powdered termite mound, mixed with water to a thick paste, was applied to sores or spear wounds. It was also eaten as a palliative for stomach aches and diarrhoea. The inner layers of termite mounds were burnt to produce an inhalant vapour. There is also a record of fly larvae from blown meat being placed in a suppurating ear, just as maggots were sometimes used in the U.S.A. for the treatment of chronic osteomyelitis wounds long before the advent of modern antibiotics.

Insects as Food

Australian native plants, especially species of *Eucalyptus* and *Acacia*, have proved to be an extremely valuable resource for world forestry. On the other hand, the only native plants to this day to have gained wide acceptance overseas as a source of human food are the eastern Australian macadamia nuts (*Macadamia integrifolia* and *M. tetraphylla*). In the relatively harsh Australian environment where native grass seeds are small and only available for brief periods and many fruits are woody, the semi-nomadic hunting and gathering habits of the Aborigines, and the fact that they had little means of storing food, exposed them to irregular and sometimes prolonged periods of food shortage. At times insects may have been almost the only available food, although some were always regarded as special delicacies. It seems that most soft-bodied insects that were available in quantity were eaten and that they were, therefore, of considerable dietary importance. A number of insects are represented in Aboriginal religion as totems and special ceremonies were performed to promote their abundance. Among the highly prized were several species of honeypot ants, the honey stores and brood combs of stingless bees, a number of species of witchety grub, the bogong moth and the sweet manna (honeydew) of various lerp insects.

The early summer migration of the bogong moth, *Agrotis infusa*, to the high country south and west of Canberra has been described on p. 69. Until about the middle of last century, Aborigines from tribes in the Snowy Mtns region came in numbers each year to feast for several months upon the millions of moths assembled in the small caves and crevices on the mountain tops (Fig. 9.1). The moths were knocked with hands or sticks from the roofs and walls of their resting places on to sheets of bark or skins. They were cooked in hot ashes, just enough to singe the wings, legs and scales, and then winnowed. There was a strong incentive to use such plentiful and easily procured food but, although the prepared moths were said to have a sweetish, nutty flavour, the initial impact of the rich food was a challenge even to the redoubtable digestive systems of the Aborigines. Once



Fig. 9.1 Massed adult bogong moths, *Agrotis infusa* (LEPI-Noctuidae), aestivating in a rock crevice on Mt Gingera, A.C.T.

[I. F. B. Common and M. S. Upton]

they could hold their meals down they throve on them so that, when the time came for them to return to their low-land hunting grounds, they were sleek and well conditioned. The bodies of the moths, in fact, contained about 60% dry weight of fat, with some protein and a little carbohydrate (Common 1954b; Flood 1980).

During the height of moth harvesting, when yields exceeded immediate consumption, the cooked bodies were pounded into fatty masses which remained edible for several days or, alternatively, they were smoked for longer preservation.

Witchety grubs continue to this day to be a much sought after delicacy among tribal Aborigines. Witjuti or witchety (often misspelt witchetty) is the Arabana word for the *Acacia* shrubs on the roots of which the mako or grubs of cossid moths feed. However the name witchety grub is now applied far more generally to stem-boring (Fig. 9.2) or root-feeding larvae belonging to many species of cossid and hepialid moths and also to larvae of certain buprestid and cerambycid beetles, the latter being known in W.A. as bardee.

In the deserts of S.A. the main species of witchety grub is the larva of the cossid *Xyleutes leucomochla* which reaches a length of 8cm towards the end of its 2-year life cycle. These larvae feed externally, within a silk lined tunnel, on the roots of *Acacia ligulata*, eating sparingly of the wood and relying mostly on the flow of sap from root wounds kept open and fresh. The larva maintains a tunnel to the ground surface inside which the pupa later ascends, piercing the lid of the tunnel just before emergence. The rising of the pupae enables Aborigines to gather large quantities of food without the labour of digging deep into the soil to obtain larvae in the feeding stage.

The larvae are often eaten raw or perhaps cooked by gently rolling them in warm ashes raked from a fire. When raw they are said to taste somewhat like scalded cream and, when cooked, like the rind of roast pork or bone marrow. Women and children spend much time

digging for the larvae and babies may often be seen with one dangling from the mouth. In some areas the grubs are said to constitute some 5% of the diet and Aborigines with access to witchety grubs are usually healthy and well nourished. In the southern half of Australia, larvae of many species of the hepialid genera *Abantiades*, *Trictena* and *Oxycaenus* are sought as witchety grubs. Among the largest is *Trictena atripalpis*, the larvae of which grow to 13 cm and live externally on the roots of the red gum at depths up to 2 m. Larvae and pupae are eaten and also the adults which emerge in numbers after the first big rain storm of summer or autumn. Then, thousands of moths emerge shortly before dusk and quantities are collected by the Aborigines before their wings have had time to expand. Those that escape this fate may mate and lay eggs, but many are also attracted to large fires lit specially for the purpose. Into these the adults fly, soon to be raked out and consumed.

Some cossid larvae burrow in the roots or stems of their host plant. One of these feeds in the base of the roly poly bush, *Salsola kali*. When larvae are about to pupate they bite through the stem at ground level and seal off the top of the hollow root to serve as a pupal chamber. Here they are readily accessible to the food gatherer, while the top of the bush is left to blow away as tumble weed.

The bardee of W.A. is the cerambycid, *Bardistus cibarius*, which ranges across to eastern Australia. Its larvae occur in the stems of grass trees, *Xanthorrhoea* spp. In Qld, larvae and adults of another cerambycid, *Eurynassa australis*, are greatly relished by Aborigines, who bake them in the ashes. Adult elytra are removed and the abdomen eaten; the flavour of the larvae is reported to be like that of an omelette. Many species of grasshopper and locust are used as food, particularly in northern Australia. There they are skewered on sharp sticks and lightly grilled.

The sugary scales of lerp insects (HEMI: Psyllidae) which feed on mulga, *Acacia aneura*, provide a relished food. The twigs bearing lerps are brushed across the lips and tongue, sometimes leaving mouths sore and bleeding and the teeth stained with insect secretions, but these are considered minor disadvantages, and the lerps are always eagerly sought.



Fig. 9.2 Larva of a witchety grub, *Xyleutes cinereus* (LEPI-Cossidae) in a stem of *Eucalyptus grandis* at Coffs Harbour, N.S.W.

[J. P. Green]

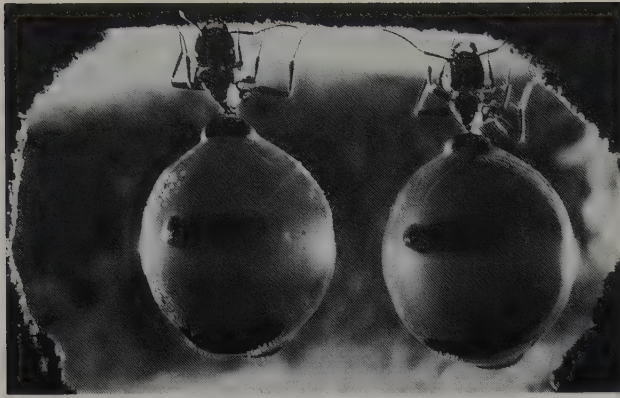


Fig. 9.3 Distended workers of the honeypot ant, *Camponotus inflatus*, (HYMN-Formicidae) hanging from the roof of their underground nest in Central Australia. [D. Clyne]

The honeypot ants of Central Australia are regarded as a great luxury and belong chiefly to the genera, *Camponotus* and *Melophorus*. The black honey ant, *Camponotus inflatus* (Fig. 9.3), lives in tunnels deep beneath mulga shrubs growing on light soil plains. Sporadic summer rain generally leads to new growth and the ants gather nectar from the flowers and honeydew from various Hemiptera. Certain workers are fed with such large quantities of the sweet fluids, which they store in their crops, that their gasters become greatly distended like small grapes. The abdominal tergites become widely separated and the yellow colour of the honey can be seen through the stretched intersegmental membranes. The honeypot workers can scarcely move, but hang in clusters from the roof of the nest. Food is solicited from these living storehouses by other colony workers during lean times. When the contents of the crop have been regurgitated to other workers the form of the replete is said to return to normal and to be indistinguishable from that of other workers. The Aborigines consume this delicacy by holding the honeypot workers by the head and thorax and biting off the greatly distended abdomen. This releases the slightly acid nectar content which is savoured as it flows over the tongue.

Another source of honey is 'sugarbag', the irregular comb of the stingless native *Trigona* bees which commonly nest in hollow gum trees. One type of honey is viscous and dark in colour, another more liquid and paler but both have a distinctive, slightly acid taste. The waxen cells containing the honey are rounded and about 6 mm in diameter; similar cells contain pollen and a third, somewhat smaller type, the brood. The whole mass, including many bees, is scooped out into a piece of bark and avidly consumed.

Insects and Aboriginal Art

Traditional Aboriginal art plays an important part in spiritual life and is a key component of many ceremonies, but its aesthetic value is also important. In European eyes, however, much traditional Aboriginal art is highly stylised and often abstract. Except for rock engravings and a few rock paintings, which have survived because of

special preservation conditions and which may date back at least 10 000 years, little surviving art (most of it employing white pipeclay, red and yellow ochres and charcoal) is more than a few hundred years old. Insects appear in a small but significant proportion of bark paintings, but less frequently in rock paintings. Prominent in both are human or spirit figures, marsupials, fish, reptiles and birds as well as stylised waterholes and campsites. The portrayal of insects is decorative and anatomical details are not recorded accurately, so the uninitiated entomologist can do little more than guess the order to which the insect belongs. Because of the powers of detailed observation of Aborigines it must be presumed that the ways in which insects are portrayed are intentional and that they have more than a decorative significance (Fig. 9.4). Insects portrayed include the sugar bag (stingless bee), the honey pot ant, witchety grubs, hairy caterpillars, grasshoppers, praying mantids, cicadas, flies, moths and butterflies, but the selection of what is illustrated is greatly influenced by the special designs 'owned' by the artist, their spiritual significance, and the importance of the insect in his area.

In Arnhem Land bark paintings, the sugar bag theme appears to be the most frequently used insect motif, partly because of the importance of honey in the diet, but also because of the parallel between the hollows in trees in which the bees often nest and the mortuary use of hollow logs in this region. The stingless bees responsible for collecting the honey are seldom shown, although the

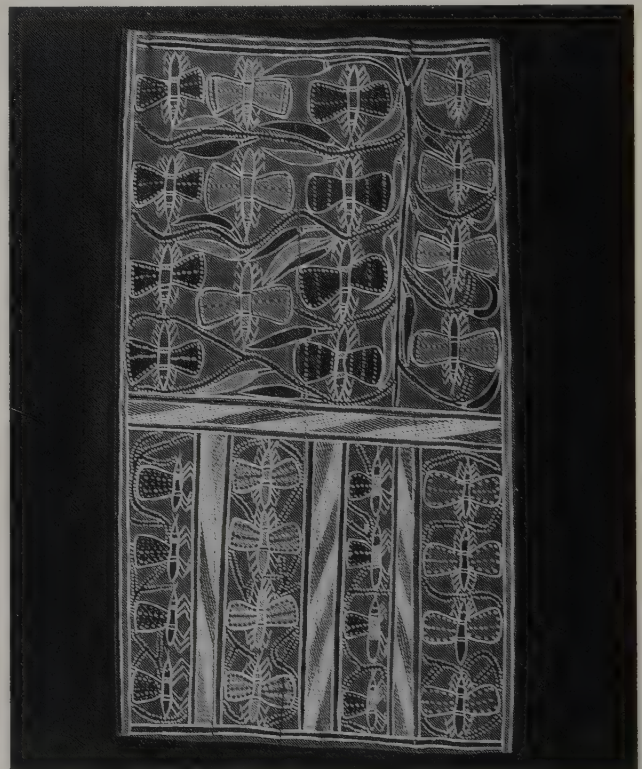


Fig. 9.4 A bark painting by Binyiniwuy of Milingimbi, N.T., depicting part of the sugar bag totem of the Gupapuyngu people. It shows bees, diamond-shaped honeycomb, butterflies and pollen from flowers.

[Photo by J. P. Green]

comb, represented as having diamond-shaped cells, always is, together with its contents—honey, pollen or brood. Often the entrance hole into the nest in a tree is depicted as a circle and sometimes with it a stone axe for excavating. Diamond-shaped cells are used in other less explicit contexts to denote the sugar bag totem. The sugar bag theme is also known in rock paintings from the Kimberleys, W.A., and from Cape York Peninsula in North Qld. As for other insects in rock art, grasshoppers are known from Kakadu National Park, N.T., and, in a small series of rock paintings at Gudgenby in Namadgi National Park, A.C.T., there is a stylised outline that is claimed may represent a bogong moth. A large number of representations of moths is also known from the Flinders Is group and Bathurst Heads in north-eastern Qld.

Rock paintings decay from natural weathering. In the past they were from time to time retouched or white-washed over and repainted, but since the disruption of Aboriginal society by European settlement this process has largely ceased, in part because the art is owned by individuals no longer in the region and no one but the traditional owners may carry out the repainting. In addition to damage by weathering, wasps deface the paintings by building their mud nests on the painted surfaces and termites construct covered galleries over the rockface. These overlays by insects are often difficult or impossible to remove without dislodging ochre. Traditionally the necessary repairs were part of the retouching process. Mud-dauber wasps, of which *Sceliphron laetum* (Sphecidae) is the most important, tend to build their nests near existing nests, so removal of the latter helps to protect an art site. Plastic strips impregnated with the slowly dispensed, volatile insecticide, dichlorvos, give added protection for a few months against nest building. The construction of termite galleries (most frequently by *Coptotermes acinaciformis* and *Ephelotermes cheeli*) can be prevented or discouraged by killing the colony responsible or by establishing a barrier of persistent insecticide, which may often be difficult in view of the nature of the terrain.

PRE-1770 EUROPEAN KNOWLEDGE OF AUSTRALIAN INSECTS

The first known record of an Australian insect dates from September 1606 when Diego de Prado, a companion of L. V. de Torres, described 'great quantities of flies' in the Torres Strait islands (see Waterhouse 1971 for this and later references). The next record is from François Pelsaert, who was wrecked in the ship *Batavia* on the reefs off modern Geraldton, W.A., in June 1629. In his 'sad daily notes' he tells of their vain search for water on the mainland and goes on 'the country was flat again, without trees, foliage or grass except for high anthills thrown up of earth, which in the distance were not unlike the huts of people. Was also such a host of flies, which came to sit in the mouth and the eyes, that they could not be beaten off'.

Early in January 1688 William Dampier wrote of the Aborigines on the north-western coast of W.A. near Roebuck Bay: 'Their Eye-lids are always half closed to

keep the Flies out of their Eyes; they being so troublesome here, that no fanning will keep them from coming to one's Face; and without the Assistance of both Hands to keep them off, they will creep into one's Nostrils, and Mouth too if the Lips are not shut very close'. On his second voyage, in 1699, to the same area of New Holland, Dampier wrote of the Aborigines: 'And these were much the same blinking creatures (here being also abundance of the same kind of flesh-flies teizing them)' and later '... we were sadly pester'd with the Flies, which were more troublesome to us than the Sun, tho' it shone clear and strong upon us all the while, very hot'.

A little earlier, in January 1697, William de Vlamingh wrote of the Swan River, near Perth, W.A. 'but in the daytime one is terribly tormented with the flies'. To complete the record, Jean Etienne Gonzal visited northern Australia in 1756 and named Vliegenbaay (Bay of Flies) in the Gulf of Carpentaria.

It is easy to recognise in these descriptions the bush fly, *Musca vetustissima*, which was clearly present in great abundance then as it often is today (Fig. 9.5). Its main breeding ground was probably human and dingo faeces, with the dung of larger herbivorous marsupials nutritive and moist enough occasionally in spring and autumn to permit larval development.

COOK'S VOYAGE TO AUSTRALIA

The earliest record of an Australian insect on Cook's first voyage was in the Journal of Joseph Banks on 16 April 1770 at about 39°S latitude in the Tasman Sea: 'Our second Lieutenant observed a small butterfly as he thought'. Although a landing was made at Botany Bay near Sydney on 29 April, the next mention of insects was on 4 May, on the eve of departure: 'The day was calm and the mosquitoes of which we have always had some more than usually troublesome'. Strangely there was no mention of the insects known to have been collected at that time. These were described by Fabricius in 1775 and included the beautiful blue-speckled diamond beetle living on wattle trees, *Chrysolopus spectabilis*, a female of the common brown butterfly, *Heteronympha merope*, and the reddish



Fig. 9.5 Bushflies, *Musca vetustissima* (DIPT-Muscidae), resting on a man's back, Esperance, W.A. [J. Feehan]

bulldog ant, *Myrmecia gulosa*. Fabricius also described our two common blowflies *Calliphora augur* and *Calliphora stygia*.

The next spot at which a landing was made was Bustard Bay, north of Bundaberg, Qld, where, on 23 May, Banks wrote of the 'great many Mangrove trees in the branches of which were many nests of Ants, one sort of which were quite green. These when the branches were disturbed came out in large numbers and revenged themselves very sufficiently upon their disturbers, biting sharper than any I have felt in Europe. The Mangroves had also another trap which most of us fell into, a small kind of Caterpillar, green and beset with many hairs; these sat upon the leaves many together ranged by the side of each other like soldiers drawn up, 20 or 30 perhaps upon one leaf; if these wrathful militia were touched but ever so gently they did not fail to make the person offending them sensible of their anger, every hair in them stinging much as nettles do but with a more acute tho less lasting smart'.

The first Australian material of the green tree ant, *Oecophylla smaragdina*, is now in the Banksian collection in the British Museum (Natural History). The caterpillars were probably of a limacodid cup moth.

Somewhat later Banks wrote 'In examining a fig which we had found at our last going ashore we found in the fruit of it a Cynips . . . ; a strong proof of the fact that figs must be impregnated by means of insects, tho indeed that fact wanted not any additional proofs'. The 'Cynips' was a chalcidoid wasp.

At Thirsty Sound, north of Rockhampton, on 29 May, Banks wrote: 'Musketos that were likewise innumerable made walking almost intolerable' and of gum trees 'on the branches of them and other trees were large ants nests made of Clay as big as a bushel . . . the ants also were small and had whitish abdomens'. This clearly refers to termites. 'In another species of tree . . . a small sort of black ant had bored all the twigs and livd in quantities in the hollow part where the pith should be, the tree nevertheless flourishing. . . Insects in general were plentifull, Butterflies especially'.

During June and July, at the Endeavour R., insects were again mentioned by Banks: termites' nests 'pyramidal, from a few inches to 6 feet in hight and very much resembled stones' and when camping ashore the 'Musquetos . . . spard no pains to molest (us) as much as was in their Power; they followed us into the very smoak, nay almost into the fire'. It was here, on 4 August, that Cook made his only mention of insects (termites) in his Journal. 'The whole country abounds with an immense number of Ant Hills, some of which are 6 or 8 feet high and more than double that in circuit'. Sydney Parkinson's Journal also refers at the Endeavour R. to 'a small culex or fly, which is not bigger than a grain of sand; the bite & sting of which was venomous, and caused protuberances on the skin which itched violently.' This is not, as might be supposed, the origin of 'sandfly', a term used by Anson thirty years earlier (in 1740) at the island of St Catherine's off Brazil: 'the Muscatos . . . were succeeded by an infinity of sand flies'.

In spite of Banks's statement that there were 'but few sorts' of insects, Fabricius described in 1775 in his *Systema Entomologiae* 212 Australian species from Cook's first voyage and more were described later.

THE FIRST FLEET

The First Fleet of 11 ships set out from Portsmouth in May 1787 via Rio de Janeiro and Cape Town to land in Botany Bay in January 1788 in order to secure eastern Australia as an English colony and to establish a penal settlement. Ships stores had been brought from England and also loaded en route to provide food for the thousand or so mouths of the young colony. However, it was essential for these stores to be supplemented as soon as possible by locally-grown wheat, rice and other crops. Unfortunately most of the grain sown in the first season's crop did not germinate because of damage by grain insects and unsatisfactory storage conditions during its long voyage in the holds of ships. Graphically, it was written ' . . . every grain of rice was a moving body from the inhabitants lodged within it' (Tench 1793). Wheat, from England in particular, had been relied upon, but much of what did manage to grow was so heavily and unexpectedly attacked before maturity by hordes of army-worms (probably larvae of the moth, *Spodoptera exigua*) that only 40 bushels resulted from the first harvest. Insects thus contributed in no small measure to the severe food shortage that was so critical in the first few years of the young colony.

BITES, STINGS AND ALLERGIES

Bites, as the term implies, are inflicted by mouth-parts, whereas stings result from the injection of venom produced by special glands situated either at the posterior end of the abdomen or at the base of stinging hairs. Detailed accounts of ill effects from both are given in Lee (1975) and Southcott (1978, 1986, 1987) and information on structure of mouth-parts is to be found in the respective taxonomic chapters of the present book.

Bites

Cockroaches, with their generalised, mandibulate mouth-parts, have occasionally been reported to pare away skin of the feet of sleepers who, on awakening, find the soles of the feet painful to walk upon. However, except for nips produced by a variety of chewing insects, which may occasionally draw blood, conventional bites are generally of minor consequence. Injurious contacts of insects with humans are most commonly the result of attack by blood-sucking species. Two elements are involved, the penetration of the skin by the mouth-parts and the introduction of saliva. The saliva sometimes has an anticoagulant action and often contains allergenic materials, so that the effects of the bites are due either to a mechanical or a chemical cause or both, with results ranging from no apparent skin response to weals, papules, vesicles and urticarial rashes of varying intensities.

Amongst the biting insects in Australia there are five blood-sucking ectoparasites intimately associated with humans, three lice, a bed bug and the human flea. If all ectoparasitic arthropods living on humans are included, there are three additional species, the scabies mite, *Sarcoptes scabiei*, the sebaceous gland mite, *Demodex brevis*, and the hair follicle mite, *D. folliculorum*.

In addition to the above, there are some flies and a few fleas that suck human blood. Each of these insects has piercing mouth-parts typical of its respective group, together with a cibarial and sometimes a pharyngeal pump for sucking the blood.

The species of lice (Anoplura: Pediculidae) that are parasitic on humans in Australia are *Pediculus humanus*, the body louse, *P. capitis*, the head louse (see Chapter 4), and *Phthirus pubis*, the crab louse. The latter is usually found in the pubic hairs, but may also occur in coarse hair on other parts of the body. These species are the only blood-sucking insects that live permanently on the human body. Their feeding causes local irritation and induces scratching. Painful lymph nodes in the neck are frequent in children with head lice, and feeding by body lice may produce numerous small red papules.

The bed bug, *Cimex lectularius*, is an obligate, blood-sucking parasite of humans. It lives in human habitations near sleeping sites and leaves these daytime refuges to feed at night. It was introduced to Australia after European settlement and, although far less common since the advent of modern organic insecticides, it still occurs in poorer, overcrowded dwellings. The tropical bed bug, *C. hemipterus*, which also lives on humans, does not occur in Australia. The bed bug feeds rapidly, becoming engorged in a few minutes. It characteristically makes several feeding punctures each a short distance apart in a linear arrangement. The bites are not usually felt, nor is there a preference for any particular site on the body. Some people are unaffected whereas others react with marked swellings and intense local irritation at the site of the bite.

Two introduced fleas commonly infest people in Australia, the human flea, *Pulex irritans*, and the cat flea, *Ctenocephalides felis*. The former occasionally attacks domestic mammals. The introduced dog flea, *C. canis*, attacks humans less frequently than the cat flea. Homecomings of owners and their pets after an absence of a few weeks or more may lead to several days of spectacular attacks on the lower part of the legs by large numbers of fleas. These have been lying dormant in their pupal cases after moulting to become adult, a condition in which they may survive for many months, and they are eventually activated by vibration. Flea plagues occur from time to time and are usually associated with periods of warm, humid weather. Less frequently, humans may also be bitten by fleas associated with other mammals, such as the oriental rat flea, *Xenopsylla cheopis*, the notorious vector of bubonic plague. Flea bites characteristically result in lumps which may itch for several days, but some individuals do not react. In children, fleas may cause a condition known as papular urticaria, although this is commonly ascribed to a food allergy, particularly

when one reactive child in a family has urticaria and another child, unreactive to fleas, has none.

Although there are occasional, incidental bites by various Collembola and Thysanoptera and by members of a few families of Hemiptera (especially Miridae, Reduviidae and Lygaeidae) the only bites commonly inflicted on humans, other than those by their ectoparasites, are by Diptera. By far the most frequent are by mosquitoes (Culicidae) and biting midges or sand flies (Ceratopogonidae), although members of the Simuliidae, Psychodidae, Rhagionidae, Tabanidae (March flies) and Muscidae are annoying at times.

During feeding, members of some families typically use their mouth-parts for relatively deep puncturing of the skin, which allows them to feed from blood capillaries (e.g. the female mosquito—the male is not blood sucking), whereas members of other families lacerate the surface of the skin and feed from the pool of serum or blood that exudes (e.g. Ceratopogonidae, Simuliidae). Pain caused by the penetration of the mouth-parts varies greatly. The fine stylets of many mosquitoes may enable them to feed without inducing pain, at least on body surfaces where there are relatively few nerve endings. Even in such situations, however, simultaneous, multiple biting generally evokes compulsive swatting. *Phlebotomus* (Psychodidae) generally feed without detectable pain and some individuals are unaware of the bite of *Culicoides* (Ceratopogonidae), although others feel it. On the other hand, the bites of Simuliidae are always painful, as are those of March flies and stable flies (*Stomoxys calcitrans*: Muscidae). As with other biting insects, there is a wide variation in response to bites: some individuals respond with fierce skin reactions, notably if there have been multiple bites by sand flies, and large weals, each surmounted with a vesicle, may be intensely itchy for days.

Stings

Stings are commonly associated with bees, wasps and ants (all Hymenoptera), although they may also result from the venom contained in the sharp, urticating hairs of some lepidopterous larvae. Immediate pain out of all proportion to the extent of the mechanical wound is always felt and the reaction to stings of some Hymenoptera may be severe enough to lead to death.

The stinging apparatus of Hymenoptera is present only in the female and consists of glands near the tip of the abdomen. These glands usually discharge through the ovipositor. The best known stinging organ is found in the worker of the introduced honey bee, *Apis mellifera*. The ovipositor is modified to form an elongate, apically-barbed sting, comprising a dorsal stylet sheath and two ventrolateral stylets, these three enclosing the poison canal. Two types of gland are associated with the sting, paired acid glands and a single alkaline gland and these discharge into a large poison sac. This sac, together with the barbed sting embedded in the flesh, is usually left behind when the bee is brushed away and the sac may go on contracting and injecting poison for several seconds.

Humans probably experience more stings from the honey bee than from all other insects combined. Often

there may be only a slight local reaction to a single sting. However, if this is received on the tongue or throat, alarming swelling and even asphyxiation may follow. When a series of stings are received an allergy to bee venom may develop (see later).

The native paper nest wasps of the genera *Polistes* and *Ropalidia* can inflict painful stings, which are followed by intense itching, sometimes lasting for several weeks. The European and English wasps, *Vespula germanica* and *V. vulgaris*, which usually nest in the ground, also sting viciously. Their habit of alighting on sugary food or entering opened bottles or cans of drink has led to stings in the mouth or throat, some of which have been fatal.

The stinging apparatus of ants varies greatly in complexity. In some species, such as *Oecophylla smaragdina*, the glands open at an orifice without a penetrating apparatus and the venom is ejected on to wounds made by the mandibles. At the other extreme, ants that are notable for their penetrating stings include the greenhead ant, *Rhytidoponera metallica*, often found in lawns, and the bulldog ants, *Myrmecia* spp. The latter administer their sting by grasping the skin with their long curved mandibles to give the firm leverage required to drive the sting, at the tip of the flexed abdomen, deep into the tissue. Their sting is particularly painful and the unwary are likely to receive multiple stings if a nest is disturbed. Repeated stings may lead to severe sensitisation and deaths have been recorded.

All larval Lepidoptera bear segmentally arranged hairs. Some species appear relatively hairless, whereas others have a dense covering. The harmful species occur among those with conspicuous hairs or spines. The stinging hairs, which are generally shorter and stiffer than the others, each has a poison-producing cell at the base and a cavity extending up to the sharp, sometimes barbed tip. Casual contact with these hairs allows them to penetrate the skin, whereupon the tip breaks, releasing the poison.

The toxin in the stinging hairs is still retained in them in the moulted cuticle. Prior to pupation the last instar larva may work its stinging hairs through the silken cocoon it has spun so that they stick out, thereby giving it added protection. Poisonous hairs like this are well developed in larvae of the gumleaf skeletoniser, *Uraba lugens* (Noctuidae: Nolinae), which feeds on the leaves of a number of eucalypts, notably the river red gum, *Eucalyptus camaldulensis*. Each abdominal segment has ten tubercles, two ventral and four lateral, carrying barbed tapering hairs, and also four dorsal tubercles bearing stiff, brown-tipped, poison-containing bristles. When these bristles touch the skin they cause a sharp stinging sensation and a weal results. Stinging is caused even by the poison hairs of newly-hatched larvae as well as by those of moulted cuticles of all instars.

Stout poisonous spines are well developed in species of *Doratifera* (Limacodidae). The slug-like larvae of the cup moths, *D. oxleyi* and *D. vulnerans* which are widely distributed in south-eastern Australia, feed on leaves of eucalypts and a range of ornamental trees and shrubs. They have two anterior and two posterior pairs of dorsal protuberances each bearing eversible rosettes of brightly

coloured, stinging spines. When disturbed, the larvae erect the sea anemone-like rosettes of spines which cause painful stinging when brought into contact with human skin, and leave large, flat weals (Fig. 9.6).

Caterpillar Hair Dermatitis

Many species of moth larvae bear sharp, non-venomous, barbed setae which cause human dermatitis in Australia (Southcott 1987). They occur mainly in the families Anthelidae, Eupterotidae, Notodontidae, Lymantriidae and Arctiidae. All of the species concerned have densely hairy bodies. If the hairs make contact with the body surface, the tips break off after penetrating the skin, resulting in intensely itchy dermatitis. This may be relieved by removing the hairs with fine forceps or adhesive plaster. Severe effects are produced when hair fragments lodge in the eye. Since detached hairs occur in each moulted larval cuticle and also woven into the pupal cocoon, contact with a living caterpillar is unnecessary. Indeed the majority of cases of dermatitis result from airborne fragments.

Two common species causing rashes in eastern Australia are the bag-shelter moth, *Ochrogaster lunifer* (Notodontidae), and the mistletoe browntail moth, *Euproctis edwardsii* (Lymantriidae). The gregarious hairy larvae of *O. lunifer* live in silken bags spun in the branches of the boree, *Acacia pendula*, and of its other food plants. The bags contain the larvae, their dried faeces, cast larval cuticles and broken-off hairs. The larvae are processionary and leave the bag at night to feed. Their reddish brown hairs are barbed and, when fractured, readily work into the skin. Even sitting near a tree where bags are hanging can have unpleasant consequences, and handling the bags leads to multitudes of hair fragments gaining access to any exposed part of the body, with dire results.

Adult Scale Dermatitis

The scales of adult Lepidoptera are modified hairs, but the rashes they have often been reported to cause are probably most often due to the adults carrying away with them some larval hairs when emerging from the cocoon. However, certain scales from females of the white rice stem borer, *Scirpophaga innotata* (Pyralidae), can cause

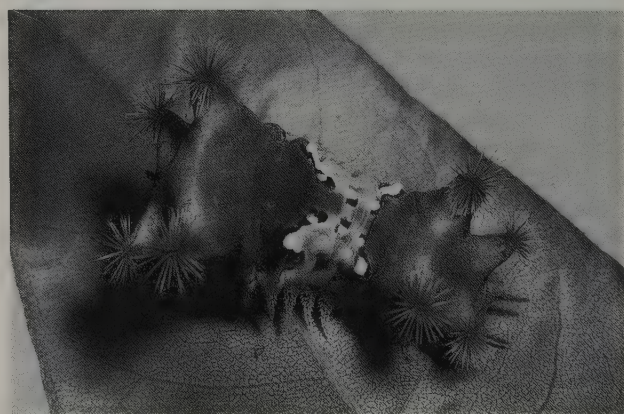


Fig. 9.6 Larva of the cup moth, *Doratifera vulnerans* (LEPI-Limacodidae), showing everted rosettes of stinging spines. [R. Jessop]

unpleasant skin irritation and hay fever. The deciduous scales responsible appear to be those borne in a large tuft at the posterior end of the abdomen.

Allergies

Most adverse effects of insects on humans result from allergies. Inhalant allergies are frequently caused by insects that produce easily detachable scales or hairs and common sufferers are entomologists and others with occupational exposure to insects (Bellas 1981). Detachable scales and hairs are notable in the Lepidoptera, Thysanura, Trichoptera and in some Diptera and Coleoptera. However scales are not an essential factor in causing respiratory allergy, which may equally be caused by fragments of faeces, of moulted cuticle and of dried insect bodies, especially of locusts (Orthoptera), Blattodea and Ephemeroptera.

Fragments of dead insects, such as flies and clothes moths, are among the allergenic materials in house dust which produce asthma, hay fever and other adverse effects. However, the main components are generally live or dead mites, particularly the house dust mite, *Dermatophagoides pteronyssinus*.

Allergic reaction is also a major factor in human reaction to stings by bees, wasps and ants and also to bites by mosquitoes, sand flies and fleas. The abrupt and generalised symptoms of anaphylaxis are characteristic of allergic sensitisation and are not related to the inherent chemical toxicity of insect venom. The venoms of Hymenoptera contain many non-allergenic amines and peptides, such as histamine and kinins. These have inflammatory and vaso-active properties which contribute to the local skin reaction. In honey bee venom the three allergenically important proteins are phospholipase A₁, hyaluronidase and acid phosphatase, of which the first is the most important. These allergens are distinct from, and have little cross-reactivity in humans to, the three major allergenic proteins in vespid venoms, phospholipase A₂, hyaluronidase and antigen 5, of which the last is the most active. It is possible to protect hypersensitive individuals against potentially lethal stings by a prolonged course of immunotherapy.

Allergic reactions to bites are primarily caused by components of the saliva which is injected both during stylet penetration and the feeding process. Although there are exceptions, two basic types of reaction occur, one immediately after the bite and the other hours or even days later. The usual pattern is for no reaction to occur on the very first bite by a particular species, or at least no more reaction than to a puncture by an aseptic probe of equivalent size. Sensitivity to the salivary secretion is developed on subsequent bites and a sequence of immediate and delayed reactions commonly occurs. After a few bites a delayed reaction is observed, often about a day later. Further bites lead to both an immediate and a delayed reaction. As a succession of further bites is experienced, the delayed reaction fails to appear but the immediate reaction persists. Eventually, after prolonged exposure to bites, both reactions fail to appear.

Defensive Secretions

Toxic or repugnatorial secretions are produced by dermal glands (p. 92) of many insects, especially Hemiptera, Blattodea and Coleoptera (Monteith and Argent 1987). These provide a defence against various natural enemies, in particular birds and other vertebrates that are insectivorous as well as against insect predators. Although many of the secretions are of little relevance to humans, others smell unpleasant and some are highly irritant if they contact the eyes or mucous membranes.

The defensive glands of bombardier beetles (p. 614) produce hydrogen peroxide, together with diphenols, the most abundant of which is hydroquinone. When the beetle is alarmed, as by being picked up, the mixture is impelled into a central chamber where a violent enzymatic reaction takes place, the end products being quinones and oxygen gas. The rising pressure of oxygen blows out the solution of tanning quinones from the orifice of the gland in a series of audible explosions.

The evil-smelling secretions produced in the metathoracic glands of pentatomid and coreid bugs contain a mixture of up to 18 compounds, characteristic amongst which are unsaturated aliphatic aldehydes, esters and ketones ranging in chain length from 3 to 13 carbon atoms. In the bronze orange bug, *Musgraveia sulciventris*, the main odoriferous compound is trans-2-octenal. This bug can eject its highly irritating secretion many centimetres into the eyes of a would-be attacker, causing great pain to vertebrates. Bug secretions commonly contain unsaturated ketones and other compounds that rapidly turn the skin brown.

INSECT TRANSMISSION OF HUMAN DISEASE

The habit of blood-sucking insects of feeding successively on a number of individuals provides an ideal opportunity for the transmission of diseases from one human to another. Mosquitoes are well known around the world as disease transmitters, although they play a very minor role nowadays in this respect in Australia. In most cases there is some form of cyclical development of the disease organism in the mosquito. Neither lice nor *Phlebotomus* (DIPT) serve as vectors in this country as they do overseas.

Although there were periods in the past when malaria, both benign (*Plasmodium vivax*) and malignant (*P. falciparum*), was widely endemic in northern Australia, this is no longer so. Even localised outbreaks are now rare and invariably follow the arrival from overseas of a malaria carrier into an area where there are suitable vectors. The principal vector in Australia is the anthropophilic '*Anopheles farauti*' (see Chapter 4), which tends to be associated with man. It occurs in coastal Qld from Ingham northwards and also in the N.T. *Anopheles amictus hilli* has also been incriminated in transmission of malaria in northern Australia. The only other proven vector is *Anopheles annulipes*, which is less closely associated with humans and has only seldom been involved. Its distribution extends far into the cool temperate regions of

Australia where malaria transmission has occurred, but only very occasionally.

Elephantiasis (filariasis) results from the blocking of lymph ducts by a filarial worm, *Wuchereria bancrofti*, which is transmitted during feeding by the introduced *Culex quinquefasciatus*, although even this mosquito is not a particularly effective vector. Filariasis dates back in the Torres Straits islands to well before European settlement, but it is not known to have occurred on mainland Australia until long after Europeans arrived and introduced labourers from China and the Pacific. Filariasis was common in some areas of Qld for several decades before and after the beginning of this century. It is no longer known to occur in Australia, although it is still present in the island arc to the north and east. Its disappearance from Australia is held to be due to the great reduction in *C. quinquefasciatus* breeding grounds. Typically, these are still or slowly moving water, richly polluted with nutrients from septic tanks or excreta of domestic animals.

The virus causing dengue fever is transmitted in Australia by *Aedes aegypti*, a cosmopolitan, introduced mosquito which breeds in containers and is closely associated with dwellings. This vector is now restricted to Qld, although formerly it extended well into N.S.W. and the N.T. Epidemics of dengue occurred from time to time until the mid-1950s but, since then, control of *A. aegypti* breeding grounds, widespread screening of houses, and the use of sprays and repellents have greatly reduced its distribution and abundance. This has led to dengue no longer being endemic in Australia. Where cases occur from time to time, these are due to infected travellers re-introducing the virus from the Pacific or South-East Asia.

The only mosquito-transmitted diseases still endemic in Australia are the arboviruses. The most serious, and occasionally fatal, disease is Australian (formerly Murray Valley) encephalitis, which has been isolated repeatedly from *Culex annulirostris*. Epidemics have occurred over the years at irregular intervals in summer and autumn in the watershed of the Murray-Darling river system, although several outbreaks were more extensive. They follow abnormally high spring rainfall leading to flooding and massive breeding of *C. annulirostris*. Although it was once thought that the virus was reintroduced by water-birds migrating in from the north, it now appears that it can survive in isolated foci of the insect vector in which it is transmitted transovarially from one generation to the next.

Epidemic polyarthritis is caused by Ross River virus, which is transmitted by several species of mosquitoes, particularly *Aedes vigilax* and *Culex annulirostris*. It occurs from time to time in Qld and N.S.W., where the major animal reservoirs appear to be mammals.

Sindbis virus is the virus most commonly isolated from wild-caught mosquitoes, especially *C. annulirostris*, in the Murray-Darling basin. Although it causes epidemics in South Africa, clinical cases are rare or unrecognised in Australia.

Murine typhus is due to a rickettsia harboured by rodents in some regions, such as the Darling Downs in

southern Qld, where rats are commonly associated with silos and grain warehouses. It is transmitted to humans by the flea, *Xenopsylla cheopis*.

Non-biting flies and other insects closely associated with humans, such as domestic cockroaches, are also involved in the transmission of human diseases, particularly those causing dysentery and typhoid fever. The house fly, *Musca domestica*, has long been regarded as efficient in transferring disease germs from place to place, not only on its feet and mouth-parts but also in its digestive tract. It deposits the germs it has picked up simply by walking over clean surfaces, by defaecation, or during the salivation and regurgitation characteristically involved in liquefying solid food before ingestion. It has been claimed that flies resulting from maggots that have bred in infested material will later transmit that infection. However, most of the organisms consumed by larvae are killed during passage through the acid mid gut, which attains a pH of 3.0 to 3.5. Furthermore, any residual larval gut contents are discharged within the larval peritrophic membrane as meconium when the adult emerges from the puparium, so that newly-emerged houseflies are often germ-free and generally pick up infections afresh from contaminated sources.

Trachoma is caused by a rickettsia-like organism, *Chlamydia*, which infects the conjunctiva and produces scarring of the cornea leading to blindness. It is common in Aboriginal communities in central and northern Australia and is thought to be transmitted by *Musca vetustissima* as well as by human contact.

INTRODUCED INSECTS

Superimposed upon the endemic Australian insect fauna is a relatively small, but economically very important, element of exotic species that has become established over the last two centuries, either as aerial plankton or as a direct or indirect result of human activities.

Insects Introduced Accidentally

The earliest European sailors to land almost certainly added several species common to sailing ships, such as cockroaches (*Periplaneta americana* and *Blattella germanica*), clothes moths, carpet beetles, flour and grain insects and the rat flea, *Xenopsylla cheopis*. However, the numbers of newcomers increased greatly with the arrival in 1788 of the First Fleet bringing, together with at least some of their associated insects, cattle, horses, sheep, goats, pigs and rabbits. It also brought many plants and seeds, including cocoa, cotton, banana, orange, lemon, tamarind, guava, prickly pear (from Rio de Janeiro) and figtrees, bamboo, sugar cane, esparto grass, vines, quinces, apples, pears, strawberries, oaks and myrtles, together with wheat, barley, rice, corn and other grains (from Cape Town). Over the next hundred years or more many additional plants and animals were brought in (mainly from Europe, eastern South America and South Africa) without any thought that some of their insect fellow travellers might become serious pests in their new country. As a result, a large number of our major insect

pests and almost all of the most important weeds in Australia have been introduced. The only important native pests that attack the introduced plant species on which our agriculture is based are widely polyphagous and thus readily able to include new plants and animals in their host range. They include termites, locusts, the Qld fruit fly (*Dacus tryoni*), various mosquitoes, sand flies, *Musca vetustissima*, pasture beetles, cutworms, armyworms, a leaf eating ladybird (*Epilachna cucurbitae*), and the lightbrown apple moth (*Epiphyas postvittana*).

Not all introductions have resulted directly from human activities, for a small but important contribution comes airborne from far away. The extremely robust wanderer butterfly, *Danaus plexippus plexippus*, a native of North America, was first reported in Australia in 1871, having flown across the Pacific, as it had many times previously. However, it was only after its larval food plants (which belong to the family Asclepiadaceae) had also been introduced, that migrating butterflies were able to establish a breeding population in Australia. It is probable that the only other introduced butterfly, the cabbage white, *Pieris rapae*, which appeared in Australia in 1937, came from New Zealand on cabbages or other brassicas carried as deck cargo. Although it is capable of dispersing widely it is not adapted to long, over-water movements. It is thought that many of the aphid pests that attack our introduced plants may have arrived as aerial plankton and this is almost certainly how the leucaena psyllid, *Heteropsylla cubana* (HEMI), a native of Central America got here. It appeared on the central coast of Qld in 1986, having first been seen in the Pacific in Hawaii in 1983, in Western Samoa in 1984 and widely in the south-western Pacific in 1985.

Nothing can prevent such airborne invasions, but a great deal can be done to reduce the chances of undesirable species being brought in by ships or aircraft. Hundreds of pests and diseases of great importance in other countries do not occur here yet. If introduced, they would cause great harm to humans, cultivated plants or domestic animals. Australia has strict quarantine laws aimed at preventing the unauthorised entry of any living plant or animal and a publicity campaign, reinforced by the spraying of aircraft on arrival, is used to discourage people from smuggling potentially infested material past the customs service.

Insects Introduced Intentionally

Domesticated insects. In many other parts of the world two insects live in close association with humans and considerable use is made of the materials they produce. These are the honey bee, *Apis mellifera*, and the silkworm, *Bombyx mori*.

In 1986 the value of honey produced in Australia by *A. mellifera* was some 20 million dollars and of bees' wax much less. However, the value of the honey bee's activities in pollinating crops was at least an order of magnitude greater. The first *A. mellifera* were brought to Australia from England in 1822 but there have been many later importations from Europe of strains that no longer occur there in pure form. Two of these still flourish in

Australia. One is the pure Ligurian strain introduced from Italy in 1882 and established on Kangaroo I., where the introduction of other strains has long been prohibited. In Tas. there is an isolated population, introduced in 1886, of what is believed to be the original European black bee. Both of these sources provide valuable genetic material for bee breeders.

The silkworm, *B. mori*, is believed to have been domesticated in China thousands of years ago and no longer occurs as a 'wild' insect. Its food plant, the mulberry tree, was introduced to Australia as early as 1796 but, although there have been a number of attempts to establish commercial silk production, all have failed. Nevertheless silkworms continue to be raised as a hobby and their larvae serve as valuable laboratory insects.

The first intentional introduction of an insect to Australia appears to have been that of a cochineal insect, probably *Dactylopius ceylonicus*, together with its prickly pear host, *Opuntia vulgaris*, from Brazil with the First Fleet in 1788. Neither insect nor plant host survived, so the hoped-for cochineal industry did not materialise.

Biological control. A particularly important use of insects is their employment as biological control agents for pests of animals and plants. The most spectacular results have come from so called 'classical' biological control, which involves the introduction of beneficial organisms from the region of the world where the introduced pest originated. There it is almost always less abundant and consequently less damaging and it generally happens that the differences in abundance in the two areas are negatively correlated with the extent to which the species is attacked by natural enemies.

All multicellular organisms are attacked by other organisms and their abundance is thereby affected, sometimes dramatically. The well-known term 'balance of nature' is not analogous with the steady equilibrium set up by an analytical chemist's balance, but rather with the tightrope walker's balance, whereby deviation from an average upright position is continuously counteracted by a reaction in the opposite direction. There is no stationary state but, instead, regular fluctuation about a mean. It is characteristic of pest species that the level of abundance attained is intermittently or permanently unacceptable to humans. Release of potential pest species from the control exerted by insect predators and parasites, following the use of broad spectrum insecticides, has highlighted the importance of biological control.

As pointed out earlier, the plants upon which Australia's agriculture is based have all been introduced, together with many other plants, some of which have become weeds. Some, but not all, of the insects associated with these plants in their native ranges accompanied them to Australia. Quite frequently it happens that the species that have become serious pests in Australia have arrived without the natural enemies that help to keep them in balance in their native range. Classical biological control aims to restore this balance by introducing organisms, when, by careful testing, it is considered safe to do so. The organisms selected for introduction are usually specific to the pest and leave non-target organisms



Fig. 9.7 The ladybird, *Rodolia cardinalis* (COLE-Coccinellidae), and two cottony cushion scales, *Icerya purchasi* (HEMI-Margarodidae).



Fig. 9.8 Larvae of *Cactoblastis cactorum* (LEPI-Pyrilidae).

[C. Lourandos]

unharméd. Once established, the control agents are self-perpetuating, although in agricultural situations care must be taken to conserve them by avoiding the unnecessary use of pesticides.

It is not possible in this chapter to discuss more than a very few of the many examples of successful biological control of great importance to Australia and the interested reader is referred to texts such as DeBach (1964), Huffaker and Messenger (1976), Waterhouse and Norris (1987), Waterhouse and Wilson (1968) and Wilson (1960) for further information.

Australia's first direct involvement in biological control appears to have been the search here in 1888 for natural enemies of the native cottony cushion scale, *Icerya purchasi*. This scale had been accidentally taken to California, where it was threatening ruin to the citrus industry. The transfer of the native predacious coccinellid beetle, *Rodolia cardinalis*, and several other beneficial insects soon brought the scale under effective natural control (Fig. 9.7). This success played a major part in awakening world-wide interest in biological control. Early forms of biological control had, of course, stretched back many centuries in other parts of the world, but it required a spectacularly successful example to fire the general imagination.

Although the biological control of a weed in Australia was suggested as early as 1899 for prickly pear

(*Opuntia*), it was not until 1903 that work commenced. Two major pest species, *Opuntia inermis* and *O. stricta* from Central America had long been spreading in eastern Australia, at least since 1839 and 1870 respectively. By 1925 these and several other pest cacti already occurred on some 25 million hectares of pastoral and agricultural land, an area as large as England, Scotland and Wales combined. The infestation was spreading rapidly and about half of the area occupied was so densely covered as to be useless. An extensive study in the Americas revealed over 150 insects living on cacti, many of which were found to be incapable of attacking other plants. Of 48 species brought to Australia, 13 were established, among them a moth, *Cactoblastis cactorum*, the caterpillars of which tunnel in the thick, fleshy cladodes of the pest (Fig. 9.8). *Cactoblastis* was established in 1925 and within a few years it caused vast areas of prickly pear to collapse (Figs 9.9, 10). The two main pest species have remained effectively suppressed in Qld ever since.

The green vegetable bug, *Nezara viridula*, a plant-sucking bug that attacks a wide range of crops, has spread from the Ethiopian or Mediterranean region to become a serious pest in most warm areas of the world (Fig. 9.11). Its successful biological control over most of Australia



Fig. 9.9 Typical dense *Opuntia inermis* at Chinchilla, Qld, November 1926.

[Qld Survey Office]



Fig. 9.10 The same area after destruction of prickly pear by *C. cactorum*, October 1929.

[Qld Survey Office]



Fig. 9.11 The green vegetable bug, *Nezara viridula* (HEMI-Pentatomidae), and its egg raft. [C. Lourandos]

has been of considerable value and is of particular interest in demonstrating the importance of geographical strains of parasites for obtaining successful biological control. In 1933 an egg parasite, the scelionid wasp, *Trissolcus basalis* (Fig. 9.12), was introduced from Egypt into W.A., where it soon produced a great reduction in bug abundance. The parasite was then distributed widely throughout southern and south-eastern Australia, making a considerable impact on bug populations, except in cultivated areas in inland, eastern Australia, where the cold winters affected its abundance. Further strains of *T. basalis* were next introduced from the West Indies, Italy, Pakistan and Japan. A very great improvement followed in the degree of control in subcoastal, eastern, cultivated areas. The successful biological control in southern Australia was repeated much later when bug populations developed in a new irrigation scheme in north-western Australia. *N. viridula* is now a very uncommon insect throughout Australia, except in a restricted subcoastal zone from north-central N.S.W. to South-East Qld and especially on soybeans. Observations indicate that the arrangement and height of the soybean leaf hairs interfere with the wasp's searching activities and far fewer *Nezara* eggs laid on soybean are parasitised than those on cowpea, mungbean or sunflower. The nature of crops in an area can thus materially affect the success of biological control.

After earlier attempts had failed to establish the European rabbit, *Oryctolagus cuniculus*, wild rabbits from England were eventually colonised on a property in Vic. in 1859. Within six years 20 000 rabbits had been killed on the property and they abounded also on neighbouring properties. In the next few years rabbits spread rapidly over much of the southern half of the continent, causing extensive damage to crops and pastures. During World War I, lack of manpower to undertake necessary rabbit control measures led to a massive plague of rabbits which ravaged vast areas of Australia. In places not a blade of grass remained and bushes were stripped of leaves and bark. Rabbits swarmed around waterholes like a seething carpet of brown fur. Careful testing had shown that myxomatosis, a South American virus disease of rabbits would not affect any of a wide range of native and

introduced mammals in Australia. Permission was, therefore, given to liberate it experimentally. Although the virulent strain that was released killed virtually all of the rabbits in the circumscribed populations into which it was first inoculated, the disease did not spread to adjacent rabbit populations. Successful spread only occurred, and then explosively, late in 1950 following virus liberations in the Murray Valley between Albury and Corowa. At that time spring floods had provided excellent breeding places for mosquitoes, including the dusk-biting *Culex annulirostris*. The latter proved to be an excellent vector, carrying infective virus particles mechanically on its biting mouthparts. In this way the virus was spread in the Murray-Darling river system over an area 1760 km by 1600 km within nine weeks and countless millions of rabbits were killed. Myxomatosis has since spread wherever and whenever there are rabbits and insect vectors. Suitable vectors include several mosquitoes, the native stickfast fleas, *Echidnophaga myrmecobii* and *E. perilis*, and the specially introduced European rabbit flea, *Spilopsyllus cuniculi*. As pastures recovered from the ravages of rabbits, wool and meat production increased markedly and myxomatosis continues to yield enormous returns in spite of the emergence of less lethal strains of the virus and of rabbits with a degree of genetic resistance.

In 1952 a European wood wasp, *Sirex noctilio*, was discovered near Hobart, killing trees in a plantation of the most important softwood in Australia, the introduced Monterey pine, *Pinus radiata*. *Sirex* is a minor pest in Europe, except where pines are unhealthy or have been damaged. Unsuccessful attempts were made to eradicate *Sirex* and, by 1959, some 40% of the pines had been killed. In 1961 *Sirex* was discovered in Vic. and it has since spread into N.S.W. and S.A. Until it was brought under successful biological control more than a decade later, it continued to cause significant mortality, particularly when it first moved into new areas. Female *S. noctilio* commonly drill several shafts into the trunk from each oviposition puncture. In the process they introduce a toxic mucus produced in a special gland. Even a minute amount of this mucus produces a severe, temporary setback to the tree, reducing its capacity to wall off *Sirex*



Fig. 9.12 The parasite, *Trissolcus basalis* (HYMN-Scelionidae) marking a *Nezara* egg in which it has oviposited. [C. Lourandos]

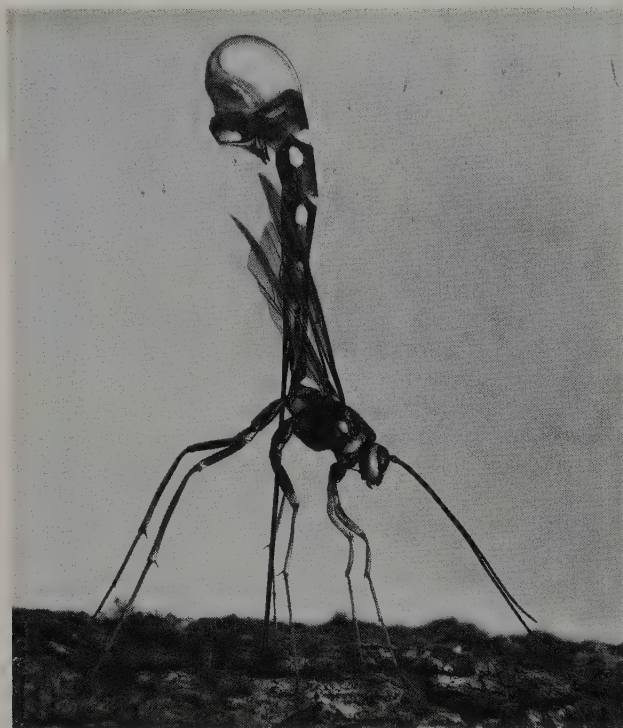


Fig. 9.13 The parasite, *Megarhyssa nortoni* (HYMN-Ichneumonidae), probing a *Pinus radiata* log with its long ovipositor in search of a *Sirex* larva. [K. L. Taylor]

eggs and an associated fungus, *Amylostereum areolatum*, known only from trees into which *Sirex* has inoculated it during oviposition. The metabolites of *Amylostereum* are capable of killing the pine tree. The rapidly-growing fungus helps to produce conditions in the wood suitable for the development of the newly-hatched *Sirex* larva and continuity of transmission is ensured by each *Sirex* female taking up a fungal culture into a special pouch, the mycangium, as she emerges from the pupa. Wasp parasites of the egg or young larva (*Ibalia* spp.) locate their hosts by detecting certain metabolites produced by the young fungus. Later, a different group of wasps (*Megarhyssa* spp., *Rhyssa* spp.) locate the larger larvae deeper in the trunk by other metabolites produced by the older fungus and associated microorganisms (Fig. 9.13). It has been possible to establish in Australia seven parasitic wasps from various regions of the northern hemisphere (including regions where our pest species, *S. noctilio*, does not occur), a fortunate circumstance rendered possible because the parasites all use the same fungal metabolites to locate their hosts. In addition, an entomogenous European nematode, *Deladenus siricidicola*, which parasitises *Sirex*, has also been established in Australia. Eggs of nematode-infected *S. noctilio* females consist of a chorion packed with juvenile nematodes. After oviposition these juveniles escape from the egg and enter a free-living phase in the wood, feeding exclusively upon the *Amylostereum* fungus, moving extensively through the timber and passing through successive cycles of multiplication. If these free-living forms encounter a

Sirex larva, infective forms are produced which penetrate the larva. After the larvae pupate the nematodes multiply rapidly and pack into the developing eggs of the female wasp. This nematode, with the assistance of the introduced parasitic wasps, has reduced *S. noctilio* to the status of a minor pest in Australia, although it may still be important for a few years as it moves into new areas, if it outstrips its natural enemies. This biological control investigation has revealed a remarkable example of symbiotic relationships.

When biological control investigations commenced in 1966, skeleton weed, *Chondrilla juncea*, was an extremely serious weed in wheat fields in south-eastern Australia. Skeleton weed is native to the Middle East and Mediterranean areas, where it is relatively uncommon and seldom regarded as a weed. It is heavily attacked there by many organisms, several of which have been introduced to Australia. By far the most destructive is the rust fungus, *Puccinia chondrillina*, which kills young *Chondrilla* seedlings and severely damages older plants. Before liberation, extensive testing of this rust demonstrated that it was specific to *Chondrilla* and unable to develop on closely related Cichoriaceae. Indeed, the strain released in 1971 was specific to the commonest form of skeleton weed, the narrow-leaf strain, and did not even attack the



Fig. 9.14 Lake Moondarra, near Mt Isa, Qld, showing floating mat of *Salvinia molesta*, December 1980. [P. M. Room]



Fig. 9.15 The same scene as in Fig. 9.14, in May 1981, after the liberation of *Cyrtobagous salviniae* (COLE-Curculionidae). [P. M. Room]

less common intermediate and broad-leaf forms which are now increasing in abundance due to lack of competition. The rust spread spectacularly and, in less than a year, infested virtually every stand of narrow-leaf skeleton weed in eastern Australia. Its damage to skeleton weed has been supplemented by the attack of an introduced gall fly, *Cystiphora schmidtii*, and a bud mite, *Aceria chondrillae*. Wheat yields have increased significantly since the establishment of these three organisms.

Salvinia molesta, an aquatic weed native to south-eastern Brazil, was probably introduced to eastern Australia as an aquarium plant in the early fifties. In the following 20 years it spread rapidly and widely, as it has done in many other countries, to infest dams, lagoons and rivers. In these it forms a compact, floating mass, which prevents the use of the water surface for transport, fishing, recre-

ation and watering of stock. Early attempts at biological control by other countries were unsuccessful because the weed had been misidentified and inappropriate insects employed. After the true identity of the weed was discovered a highly effective weevil, *Cyrtobagous salviniae*, became available from eastern Brazil and the situation changed dramatically. The first field release of *C. salviniae* took place in Australia at Lake Moondarra in Qld in 1980 (Fig. 9.14). It rapidly became established and soon produced spectacular control, reducing in 14 months the initial 19 000 tonnes of *Salvinia* to less than 1 tonne and clearing the water surface of floating weed (Fig. 9.15). Releases elsewhere in Qld were similarly successful. These excellent results have since led to the weevil being introduced to other countries, including Papua New Guinea and Sri Lanka, with equally striking results.

Australian Insects in Scientific Research

M. J. WHITTEN

First scientific contact with the immense and diverse Australian insect fauna came during James Cook's epic voyage in 1770, with Solander and Banks's brief collecting forays along the east coast of Australia. Fabricius, a Danish pupil of Linnaeus, described 212 species from the Banks collection and shortly afterwards he worked up a much larger assortment collected by Riche and La Billardi re who sailed as naturalists on the Joseph de Bruni D'Entrecasteaux expedition of 1791–94 to Tasmania and Western Australia (Musgrave 1930). These events marked the commencement of an era, lasting some 150 years, characterised by descriptive taxonomy and natural history of Australian insects. Most descriptions were performed by overseas entomologists residing outside Australia with much of the material being deposited in British or European institutions.

The history of this period is covered elsewhere (Musgrave 1930; Mackerras 1949; Marks 1983 and Chapter 8) but several developments during this period are worth documenting to assist our appreciation of the role that Australian insects were subsequently to play in influencing the course of biological research in the 20th century. Perhaps most important were the circumstances which enabled entomological research to be conducted within Australia itself, and not in the alien environs of museums in England and Europe. Central to these developments was the foundation in 1862 by William John Macleay of the Entomological Society of New South Wales with its own *Transactions*, the establishment of the Macleay Museum at the University of Sydney in 1873 and deposition of the Macleay collections in that institution, and the foundation of the Linnean Society of

New South Wales in 1874. The *Transactions of the Entomological Society of NSW* and the *Proceedings of the Linnean Society*, together with the publications of the Royal Societies in each of the six colonies, permitted ready dissemination of studies on Australian insects by resident entomologists. Thus, by the turn of the century, there was a distinguished group of amateur naturalists active in the colonies. The first salaried entomologists were appointed around 1890, and these were to meet two distinct needs: natural history (in the Museums) and economic entomology (in each of the colonies, or States after 1901). However, none of these workers, including the prolific W. W. Froggatt (see Chapter 8), used insects specifically to define principles or processes, or to validate hypotheses of any general relevance to biology. In fact they described what they saw or were able to measure; little that was done or written had any relevance other than to the material under investigation.

One of the most productive and distinguished of the amateur naturalists, although he was eventually paid a princely emolument to pursue his 'hobby', was R. J. Tillyard (Mackerras 1949; Schedvin 1987). His extensive taxonomic writings between 1904 and 1936 on modern and fossil insects were descriptive and reactive to what lay before him. His research lacked any experimental dimension or significant theoretical framework; there was no discernible underlying philosophy and his interpretation of data was non-Darwinian in conception. For example, the sole reference to Charles Darwin in his monumental *The Insects of Australia and New Zealand* relates to a species of thrips collected by Darwin near Sydney in 1836. Darwinian thinking, in fact, appears to

have escaped Tillyard and his entomological contemporaries before 1927. Indeed, the intellectual framework behind all Tillyard's taxonomic work typified more the thinking of late 18th century biology. His palaeontology indicated that he accepted evolution as a fact but nowhere did he consider the forces or processes behind evolutionary change and the profound implications this would have on classification theory. These observations are not intended to demean Tillyard's contribution to entomology in Australia and New Zealand. He was a product of an era of science that was eclipsed in Australia around 1927; but he was not destined to be an active participant of the new era. I will illustrate these conclusions more forcibly below in considering A. J. Nicholson's contributions to our understanding of mimicry amongst Australian insects and its theoretical basis, his intellectual influence on the course of theoretical ecology, and his impact on international science and on the development of biological control.

Insects as Tools in Research Overseas before 1900

Although insects were used during the 19th century in the United Kingdom and Europe to elucidate principles and define biological processes with relevance beyond the Insecta, this was more the exception than the rule before the advent of experimental biology, which did not commence in earnest until the beginning of the 20th century. For example, relatively few instances can be found overseas during the second half of the 19th century of insects being used as subjects in embryology, histology or cytology to influence the formulation of the cell-theory, the other major conceptual development complementing Darwin's revolutionary thinking in evolutionary theory. R. Leuchart used *Melophagus* (Diptera) in 1858, C. Robin used various culicines, and A. Weismann used *Chironomus* and *Musca* in 1863 to study how a syncytial phase preceded the cellular phase of the insect blastoderm, instead of the more conventional cleavage processes of other animals (for details see Baker 1948–55). In general, insect cytology did not play a prominent role in the development of the cell-theory. This is in marked contrast to the conspicuous role played by insect embryology and cytology in the 20th century (M. J. D. White 1973).

As we will see later, the recent shift in emphasis to insects rather than other animals and plants as models is partly associated with the need to rear and manipulate a convenient experimental organism, and usually under laboratory conditions. Insects have proved well suited to such treatment. Fortuitously, many insect species, particularly amongst the cultured Diptera, have also displayed attributes such as giant polytene chromosomes which have further enhanced their suitability for some current disciplines such as developmental and molecular biology.

Scharrer (1987) has argued that the value of model systems was first recognised by Owen in 1843 but, for over 100 years, models were restricted to systems which shared common evolutionary ancestry. The value of analogous biological systems was not recognised until well into the 20th century. Indeed the full power of model systems that combine analogous and homologous elements is

still not fully appreciated by biologists, and even less by medical scientists (see below).

Compared to most 19th century cytologists and entomologists, Darwin made extensive use of insects in exemplifying his theory of evolution by natural selection. He maintained active dialogue with some 80 entomologists during his working life (Remington and Remington 1961). In particular, he used insect examples in 1862 to illustrate the struggle for existence, natural selection and natural classification. Specific instances include aptery in island species of beetles, convergent evolution of British and Brazilian freshwater beetles, coevolution of flowers and insect pollinators (Darwin 1904), and slave-making ants (Remington and Remington 1961). Other than a brief reference to insect pollination of Australian orchids, a topic alluded to by R. D. Fitzgerald in his 1875 *Australian Orchids*, our insects did not feature in Darwin's evolutionary arguments, despite his brief visit to the continent in 1836.

Perhaps the most powerful use of an entomological example by Darwin to illustrate a general principle was his use of H. W. Bates's (1862) study of mimicry in butterflies from the Amazon Basin to refute the creationist arguments of Alexander Agassiz. Darwin recognised the critical importance to evolutionary theory of Bates's work on mimicry and cited it extensively in later editions of *The Origin of Species* (Remington and Remington 1961). In a letter to Bates in 1862 Darwin stated:

Dear Bates,—I have just finished, after several reads, your paper. In my opinion it is one of the most remarkable and admirable papers I ever read in my life. The mimetic cases are truly marvellous, and you connect excellently a host of analogous facts. . . I am rejoiced that I passed over the whole subject in the "Origin", for I should have made a precious mess of it. You have most clearly stated and solved a wonderful problem. . . Your paper is too good to be largely appreciated by the mob of naturalists without souls; but, rely on it, that it will have lasting value, and I cordially congratulate you on your first great work. (cited in F. Darwin 1887).

If the reader has any doubts about the genius of Darwin for extracting important principles from a welter of detail of transitory significance, a reading of Bates's paper should settle the matter.

Darwin (1863) on the same subject, wrote:

By what means, it may be asked, have so many butterflies of the Amazonian region acquired their deceptive dress? Most naturalists will answer that they were thus clothed from the hour of their creation—an answer which will generally be so far triumphant that it can be met only by long-drawn arguments; but it is made at the expense of putting an effectual bar to all further inquiry. In this particular case, moreover, the creationists will meet with special difficulties; for many of the mimicking forms of *Leptalis* can be shown by a graduated series to be merely varieties of one species; other mimickers are undoubtedly distinct species, or even distinct genera. So again, some of the mimicked forms can be shown to be merely varieties; but the greater number must be ranked as distinct species.

Hence the creationist will have to admit that some of these forms have become imitators, by means of the laws of variation, whilst others he must look at as separately created under their present guise; he will further have to admit that some have been created in imitation of forms not themselves created as we now see them, but due to the laws of variation. Prof. Agassiz, indeed, would think nothing of this difficulty; for he believes that not only each species and each variety, but that groups of individuals, though identically the same, when inhabiting distinct countries, have been all separately created in due proportional numbers to the wants of each land. Not many naturalists will be content thus to believe that varieties and individuals have been turned out all ready made, almost as a manufacturer turns out toys according to the temporary demand of the market.

Such powerful examples of insect models in the 19th century biology are not common. Entomologists, in general, were more concerned with describing what was before them, the better ones annotating interesting points of natural history. In general, biologists were not possessed of synthetic and analytical skills or experimental methodologies, and entomologists less so than most. Indeed, as a body, entomologists were slow and reluctant to accept the new order, largely introduced by Darwinian thinking and many were content with little more than 'stamp collecting'.

J. W. Douglas, in his presidential address to the London Entomological Society in 1860 described his fellow entomologists as 'Genus irritabile' and has this to say: 'Collecting has with some persons become such a mania that to form a collection, at whatever costs, appears to be the sole object of their lives' (Remington and Remington 1961).

In 1863 Darwin wrote to J. D. Hooker:

How few generalisers there are amongst systematists: I really suspect there is something absolutely opposed to each other and hostile in the two frames of mind required for systematising and reasoning on large collections of facts. (cited in F. Darwin 1887)

Elsewhere Darwin writes to Bates in 1861:

I can understand that your reception at the British Museum would damp you; they are a very good set of men, but not the sort to appreciate your work. In fact I have long thought that too much systematic work and description somehow blunts the faculties. The general public appreciates a good dose of reasoning, or generalisation, with new and curious remarks on habits, final causes, etc. etc., far more than do regular naturalists. (cited in F. Darwin 1887)

To E. Haeckel, Darwin wrote in 1867:

No body of men were at first so much opposed to my views as the Members of the London Entomological Society, but now I am assured that, with the exception of two or three old men, all the Members concur with me to a certain extent.

According to Remington and Remington (1961) the only public reaction by the London Entomological Society to

the publication of *The Origin of Species* appears to be a facetious statement in 1860 attributed to H. T. Stainton when he noted the crowding in the meeting room:

many of our members would succumb in this new struggle for existence, and those entomologists best fitted to breathe our vitiated atmosphere would have advantages over their fellows, and would become the favored race; and supposing they transmitted these qualifications to their descendants, it might happen, in the course of a few hundred years, that a race of entomologists would be produced who would positively feel uncomfortable unless in rooms crowded to suffocation.

Unfortunately, this prediction has not come to pass, and entomologists seem to demand even more breathing space than their colleagues!

The Role of Insects in 20th Century Science

Difficulties of the type experienced by Darwin with entomologists have not been a feature of 20th century science. Insect models have become widely adopted for research, and like many critical discoveries or shifts in research direction, major advances have tended to occur simultaneously and somewhat independently in separate continents. By the 1920s the now cosmopolitan vinegar fly *Drosophila melanogaster* had justified its choice in 1908 by T. H. Morgan as the model for his studies on the principles of Mendelian genetics, and for the chromosomal basis of inheritance. The vinegar fly subsequently featured in virtually every major concept that emerged in genetics and cytology, and it was a central organism in studies detailing the most significant conceptual revolution of modern biology, namely the elucidation of the physical and biological basis of inheritance (Whitten 1985). *D. melanogaster* and its relatives have been the organisms of choice in many branches of genetics and evolutionary studies for 70 years, and recent advances in molecular biology have further consolidated its position as the organism, par excellence, for studies in neurobiology, developmental biology and behaviour.

In the early 1920s H. J. Muller personally delivered some 32 mutant strains of *D. melanogaster* from the U.S.A. to biologists in the U.S.S.R. (Muller 1923). These stocks acted as a catalyst to unite the two disparate trends in Russian science; experimental biology and natural history (Adams 1980). Within the extraordinarily brief period of four years, S. S. Chetverikov had developed the first adequate account of the genetic basis for evolution by natural selection, predating his western counterparts by several years (Whitten 1985). The new genetics, almost exclusively using local insect models such as *D. pseudoobscura*, put the U.S.S.R. at the forefront of pure and applied genetics, until the discipline's abrupt termination at the hands of T. D. Lysenko two decades later (Whitten 1985). Compared to the U.S.S.R. and the U.S.A., contemporaneous influence of insect models was less spectacular in western Europe and the United Kingdom, especially in genetics and evolutionary studies, where W. Bateson, C. A. Darlington and others largely utilised plant model systems (Whitten 1985).

The Foundations of Entomology as a Science in Australia

A. J. Nicholson was appointed to the first Australian university position in Entomology in 1921 (Mackerras 1971) and he was undoubtedly the first to use Australian insects in a major contribution to biological thinking. At this point, a survey of the general state of entomology in Australia around 1921 will be helpful.

As outlined above, the magnitude and diversity of the native fauna had been recognised almost since the beginning of European settlement, and this had stimulated a vigorous taxonomic effort by a group of amateurs, and a growing handful of salaried naturalists, especially after 1891 (Mackerras 1949). However, whether intentionally or accidentally, a century of European settlement had contributed to a range of exotic weeds and insect pests. These insects, together with some native species, competed with man for food and fibre, and transmitted a range of diseases of crops, livestock and man (Chapter 9). By 1890 the colonial governments had recognised these problems in economic entomology and government entomologists were appointed in at least four States before 1900 (Musgrave 1930). By way of comparison, the U.S.A., which had been settled much longer, also began to recognise the importance of economic entomology. However, by 1867 only three States, New York, Missouri and Illinois had official entomologists (Kingsland 1985).

Thus by 1920 two important conditions for the birth of entomology as a science in Australia were realised: these were acceptance of the cultural significance of the native insect fauna, and the economic impact of exotic and native insects as an integral part of the environment as modified by Aborigines and Europeans.

On his appointment as lecturer in Entomology at the University of Sydney in 1921 Nicholson had a clear brief to train students in agriculture and science to cope during their professional life with these two aspects of Australian entomology (Mackerras 1971). Within six years Nicholson had a comprehensive grasp on the insect fauna. By 1927 his commanding familiarity and natural curiosity had led him to focus on a series of fascinating examples of cryptic and deceptive resemblance amongst native insects. The conclusions of this study were presented as a long and scholarly presidential address to the Royal Zoological Society of NSW (Nicholson 1927). Nicholson's special interest and skills in photography disposed him to recording outstanding instances of insect mimicry. This photographic record lent itself to the topic of his address, prepared with only two weeks' notice. The requirement to follow up the address with a written manuscript, again with a meagre several months for the task, caused him to concentrate his attentions not only on the phenomenon of mimicry itself but also on identifying the selective forces operating to favour the mimetic morphs. In the course of his paper significant principles emerged, for example the relief from predation resulting from mimicry or cryptic coloration shifting the pressure of natural enemies to other components of the life cycle.

Nicholson drew together his extensive material

on mimicry, integrating it with descriptions of insect mimicry elsewhere, while drawing eclectically on experimental and breeding studies by overseas workers. He proposed an evolutionary explanation for mimicry and, in so doing, provided the first adequate genetic account of mimetic change (Turner 1987).

Nicholson postulated that natural selection favoured specific major mutations which induced discrete phenotypic shifts that conferred an advantage on their possessor. The resulting mimic was more likely to be confused with an unpalatable model in instances of deceptive resemblance, or was less likely to be detected in the case of cryptic resemblance. From a genetic perspective, Nicholson provided an interpretation of the nature of spontaneous mutations; he recognised frequency-dependent selection, and displayed a penetrating insight into the process of natural selection and genetic load, or what we might now term *soft* selection.

What was to have a more immediate, and far greater impact, were the ramifications envisaged by Nicholson for population ecology and biological control. He made the critical and original observation that mimetic species appeared to be no more abundant than closely related non-mimetic species, yet they had presumably displaced non-mimetic ancestors, as a result of selective advantage. In developing his arguments as to how natural selection might operate to favour the newly arisen mimetic forms, Nicholson elaborated a general theory on the limitation in numbers of animals, and foreshadowed his later ideas on competition, and the density dependent regulation of animal populations. His mimicry studies led him to suppose that predators and parasites, rather than food supply, climate or disease, were the only conceivable factors to exercise a stabilising influence on the numbers of any insect species. Thus by 1927 Nicholson had made a significant contribution to evolutionary theory. He had provided a genetic explanation for a widespread evolutionary phenomenon *before* Chetverikov and R. A. Fisher had advanced a genetic explanation for the evolutionary process at large, *and* he had laid some vital foundation stones for the science of animal ecology. The general importance of Nicholson's paper was recognised by A. J. Turner, the lepidopteran naturalist who wrote to Nicholson from Qld in December 1927:

I was delighted to read a paper which is really constructive, which makes the way of nature clearer, and strengthens one's belief in the capacity of the mind of man to understand them. You have written lucidly, calmly and impartially, and I think your paper would have pleased old Darwin . . . Your arguments for the existence of mimetic resemblances should not have been necessary. Actually they were necessary, and being mostly from Australian insects observed in the field are interesting. Your defence of natural selection I think unanswerable. Your demonstration of the way mimetic resemblance can be conceived as a necessary consequence of causes which do not affect the existence or abundance of a species was new to me. Your reasoning seems to me perfectly sound, and the natural mechanism unveiled is very beautiful as well as intricate. Furthermore your discussion of the biological factors

which control insect populations should be very important to the economic entomologist. (CSIRO Division of Entomology archives).

In concluding his 1927 address, Nicholson reviewed his vision for the future of entomological research in Australia:

I should like to make a plea for the more intensive study of purely biological problems in Australia. We have special advantages for the study of such problems which few other countries possess and which will not be available to future generations in this country. Even within easy access from such a populous centre as Sydney there are hundreds of square miles of country still in practically its primeval condition, and this gives us unique opportunities for studying organisms in relation to their normal environment. I feel strongly that every possible use should be made of these opportunities while they remain, even if that has to be partly at the expense of taxonomic work. I do not wish to belittle the importance of taxonomic work. The long series of species mentioned and illustrated in this address which I have been unable to get identified clearly demonstrates the urgent necessity for further taxonomic work, as a large number of these are known to be undescribed species and probably a considerable proportion of the remainder are also undescribed.

Mackerras (1971), in a tribute to Nicholson, was to write:

By the late 20s lectureships (and one Chair) were established in other universities, the demand of State Departments grew steadily, and the Commonwealth established the Council for Scientific and Industrial Research . . . Young people interested in insects no longer became doctors or school teachers and devoted their leisure to their hobby; they took on appropriate degrees in a university and made entomology their profession, with ever widening fields of research and ever increasing technical and financial resources before them. It could fairly be said that, so far as Australia is concerned, Nicholson in a sense began it all.

Why Do Insects Represent Useful Tools in Biological Research?

The 'opportunity' argument. I have alluded to the shift in biological science from description to observation, prediction and experimentation around the turn of the century, and the increasing inclination of scientists to define principles and general processes, with broad relevance to other organisms and biological systems. Scientific enquiry had been increasingly fuelled by the need to explain the unknown, as it displaced religion in this particular function. Test organisms became one means to achieve this epistemological goal. Thus the choice of a suitable model organism was critical to successful science. But why insects?

The mere abundance, diversity, ubiquity and availability of potential insect subjects must have influenced many biologists to choose insect models for research purposes. Further, the pest significance of some species renders them and their relatives plausible candidates for strategic

research offering the prospect of economic benefit to industry and the community, as well as supporting more fundamental scientific work. In other words, insects can provide a real solution to a perennial pragmatic problem: who will fund the research? Similarly, the central role that Australian insects play in the natural environment, and the intrinsic fascination which insects hold for many lay persons, argues further in favour of insect models. This familiarity with insects as friend or foe in everyday life often enables the biologist to use insect examples in explaining some relevant principle or process to those who ultimately underwrite the costs of research. Thus insects provide a natural opportunity for teaching and conveying complex ideas to other scientists, students and lay persons. The value of insects in teaching, especially in the context of laboratory, experimental or natural history studies, is likewise paramount.

Suitability for laboratory and field manipulation.

Insects have many attributes that make them ideal candidates for experimental studies. Many species can be reared easily and cheaply, have short life cycles and high fecundity, and are easily manipulated in confined and manufactured spaces, on artificial or easily supplied media. Many are conducive to controlled mating and most can be subjected to a range of specified physical and chemical conditions. Furthermore, once a particular species becomes established as the organism of choice in one or more scientific disciplines, propinquity often tends to favour its choice in other areas. This is well illustrated by the history of *D. melanogaster* in the genetic studies of Morgan. Castle (1951), who was a young faculty member in the Zoology Department at Harvard University at the turn of the century, recounts the events:

One of the baffling problems of breeders in pre-mendelian days had been the effect of inbreeding and cross-breeding. What these were was a much debated question. We set out to give it an experimental test and found ready to hand a rapidly breeding little fly, *Drosophila*, being cultured in the laboratory by a graduate student as embryological material. This, he told us, would complete a cycle within a fortnight . . . The results of this work, in which five students had in successive years co-operated, were brought together and published in May 1906 . . . The important outcome of this investigation was that it called to Morgan's attention a new source of material for experimental study, not subject to the limitations of slow breeding laboratory animals. So Morgan began breeding *Drosophila* and you know the rest . . .

In some instances, detailed knowledge of an organism can suggest ways of testing ideas in unrelated disciplines. For example, the extensive knowledge of genetics and cytology of *D. melanogaster* established it as the naturally preferred animal for many studies in molecular biology, neurobiology, behaviour and development. To a lesser extent, the Australian sheep blowfly *Lucilia cuprina* has become an organism of choice for fundamental research in Australia. It is one of the few significant insect pests where physiology (Waterhouse and Stay 1955; Barton Browne *et al.* 1979), behaviour (Barton Browne *et al.*

1976, 1987; P. H. Smith 1987; Smith *et al.* 1988), biochemistry (Hackman 1986; Campbell and Birt 1972; Williams and Birt 1972; Summers *et al.* 1982), ecology (Vogt *et al.* 1983; Wardhaugh *et al.* 1988), economic entomology (Foster *et al.* 1985; Vogt *et al.* 1985), evolution, taxonomy and genetics (Thomson 1987; Foster *et al.* 1985; Waterhouse and Paramonov 1950) have been studied comprehensively. In genetics and cytology, it represents an 'outrider' to *D. melanogaster* giving a useful means of validating the principles enunciated for the latter.

As a teaching resource illustrating a diversity of principles in pure and applied entomology, *L. cuprina* offers an escape from the serendipity involved in using the cosmopolitan *D. melanogaster*. Once an insect is established as a teaching tool, its application to research problems often follows, or vice versa. The use of *L. cuprina* in teaching at the University of Melbourne during the 1970s contributed to its selection for research on the ecological genetics of pesticide resistance (Whitten and McKenzie 1981). *L. cuprina* also plays a dual role in teaching and research concerning electrophysiology and behaviour in the Entomology Department at the University of Queensland (Rice 1982) and on intermediary metabolism of eye pigmentation in the Biochemistry Department at the Australian National University (Summers *et al.* 1982).

In a similar manner, the Queensland fruit fly, *Dacus tryoni* has been a major experimental and teaching tool at the University of Sydney for over 40 years: in embryology (Anderson 1964), ecology and population dynamics (Bateman 1968; B. S. Fletcher 1973b, 1979), economic entomology (Bateman *et al.* 1966; Andrewartha *et al.* 1967), evolution, genetics and taxonomy (Lewontin and Birch 1966; Vogt and McPherson 1972; Vogt 1977; McKechnie 1974), physiology and behaviour (Barton Browne 1957; Tychsen 1975; Meats 1983; Fitt 1986; Prokopy and Fletcher 1987). Indeed, many active entomologists in Australia developed their scientific skills at the expense of *D. tryoni*.

Ethical Considerations and Animal Liberation

We increasingly devote resources and effort to destroying pest insects, and to suppression of insect populations, using a range of physical, chemical and cultural devices. These include extremes of temperature, electrocution, mechanical damage, neurotoxins, antimetabolites, growth inhibitors, incarceration, sterilants and so on. Accordingly, it might be supposed that insects have no discernible rights and so are legitimate objects for any scientific or experimental purpose, particularly one that improves human capacity to destroy pests or augment knowledge.

Recently, strong lobbies have developed in many Western countries ascribing clear rights to animals, arguing against their captivity, deliberate injury or use in experimentation for scientific or other purposes, even where clear benefit to us all is evident. Insects have not received specific attention in this debate and their use for scientific enquiry and experimentation continues without restriction. It is prudent to identify circumstances where this could be unwise or unethical, and to consider a code

of conduct for scientists aimed at reducing the likelihood that external constraints might be effected to control the use of insects in scientific enquiry. Such anticipatory action is particularly timely for two reasons. It allows entomologists to exploit the gap caused by pressure to reduce experimentation on higher animals, and secondly because insects appear to represent valid models for an increasing number of fundamental processes which exist or have counterparts in higher animals, including humans (Scharrer 1987).

Pertinent to the general suitability of insects as experimental organisms is their presumed limited capacity to experience pain or related emotions such as apprehension, anguish, frustration and so on. Surprisingly, these topics have received little attention from experimental biologists. A detailed examination of the subject by Eisemann *et al.* (1984) reaches the rather firm conclusion that on neurobiological, behavioural and general evolutionary grounds it is unlikely that insects experience pain, or any sensation akin to it. Indeed, a study of the behavioural response of insects fails to identify any adaptive value for 'pain' in insect biology.

Eisemann and colleagues argue that there is no current basis for limiting experimentation with insects on such grounds. However, they endorse Wigglesworth's (1980) advice that inactivation of the nervous system should proceed when practicable before any possibly traumatising manipulation. They argue that such a precaution 'guards against the remaining possibility of pain infliction and, equally importantly, helps to preserve in the experimenter an appropriately respectful attitude towards living organisms whose physiology, though different, and perhaps simpler than our own, is as yet far from completely understood' (Eisemann *et al.* 1984).

What Biological Systems Can Be Modelled by Insect Studies?

When we consider an insect as a tool or model in research we are really supposing that our resultant improved understanding of the process, mechanism or system under investigation has applicability to other insects, and hopefully to other organisms. Let us consider an example of this cascading effect. Identification in bacteria of a group of genes called *heat shock protein genes (hsp)*, whose protein product is induced under inimical temperatures or other stressful situations led to the prediction and eventual isolation of homologous *hsp* genes in *D. melanogaster* (see Schlesinger *et al.* 1982). In turn, Thomson (1987) supposed that such genes would be present in other insects, including two native bracken flies, *Drosophila megagenys* and *D. notha*, and that expression of *hsp* genes in these species could provide an adaptive response to rapid temperature rises in nature. He demonstrated that such genes did exist and were expressed under appropriate conditions indicating likely adaptive response mechanism in poikilotherms to sudden and unpredicted stress. In this example, *D. melanogaster* was used to model a single postulate—the widespread existence of *hsp* genes in insects, while *D. megagenys* and *D. notha* became

models for insects in general concerning the possible adaptive role of *hsp* genes. The resultant findings may ultimately have relevance to field ecology where extremes of temperature are experienced by insects, and to stored product entomology where rapid changes in temperature are unusual but can be induced as a control measure. Similar studies by Whyard *et al.* (1986) on the heat shock response in *Locusta migratoria* suggest that homologous proteins might provide thermal protection against high temperatures likely to be experienced by insects in natural environments.

Insects have been used to define the related and more general phenomenon of acclimation. For example, it is known that the responses made by *Dacus tryoni* in the short term to changes in its environment can be modified in the long term, if those changes persist (Meats 1989; Meats and Fitt 1987). The underlying molecular mechanism is not yet understood, but acclimation is known to permit either a lessened or an enhanced response to sustained environmental change. It therefore represents a survival strategy for poikilothermic animals inhabiting variable and unpredictable environmental regimes. An understanding of such processes can be of value in behavioural ecology and applied entomology, for example in quality control of insects produced under mass rearing conditions for sterile male release programs.

Given this notion of insects as tools for research, and given their general suitability for experimental manipulation, for what general processes and mechanisms are insects likely to offer themselves as valid models?

Invertebrates, including insects, have a fundamentally different body plan to vertebrates, and their sensory apparatus is radically different. Their nervous, circulatory, respiratory and digestive systems appear to be more analogous than homologous with those of vertebrates. Their general behaviour is largely deterministic and highly programmed, and seems to offer little scope for learning through experience. It might be supposed, therefore, that using insects as models, we can learn little which is applicable to other animals or plants. This would suggest that research on insects can be justified only to the extent that it assists in the control of baneful species; or illuminates our understanding of their role in natural systems, or reveals the nature of their interactions with other organisms in which we have an interest. Certainly one must recognise that the differences between vertebrates and invertebrates are not superficial—not to do so would be to ignore a major rational basis for human fascination with the insect world. However, we are beginning to perceive in insects many fundamental processes in cellular, biochemical, neurobiological, developmental and behavioural biology which have features in common with vertebrates, and which perhaps indicate an extraordinary level of conservatism at the cellular and molecular levels of biological organisation. Insects and vertebrates have independently responded to various environmental challenges by devising similar solutions. We have considered Scharrer's thesis that the study of analogous biological systems in mammals, using a more amenable insect model, can encourage the identification of new principles

unlikely to be recognised through direct mammalian studies. She illustrates this convincingly in her comparative review of the neuroendocrine system of insects and vertebrates (Scharrer 1987).

The balance of this chapter considers the dual topics of insects as objects of research, and the past and future value of insects as research tools, both in homologous and analogous modes, in the disciplinary areas of taxonomy, evolutionary studies, genetics, cytology, ecology, biological control, developmental biology, neurobiology and behaviour.

Taxonomy and Evolution

A primary objective, and the major product, of insect taxonomy in Australia should be the characterisation of the native insect fauna, and an elucidation of the general biology of its component species. Our reason for wanting to document the Australian insect fauna is not simply that it is 'a mountain we should climb just because it is there', but rather because economic benefits clearly stem from insect taxonomy. Considerable social and cultural benefits accrue as well. Wilson argues elegantly that our natural affinity for life—biophilia—is central to our humanity. '... and binds us to all living species' (Wilson 1985d). Thus to permit destruction of fauna because of avarice, neglect or apathy should be contrary to our nature, and certainly would be inimical to our broad interests. A world devoid of species diversity is an environment incompatible with human nature (Wilson 1985d). Enduring human wealth can surely be measured in terms of the numbers of species around us, and our appreciation of them. Thus to catalogue and preserve what insect species we have in Australia and to understand their adaptations, their general biology and how they interact amongst themselves and with other animals and plants groups are pursuits of enormous social and cultural significance to present and future Australians.

The task of characterising the Australia insect fauna is far from complete. It has been irreverently suggested that the rate of evolution and speciation could be outstripping the national effort by the meagre cadre of systematists in the country. On the other hand, agricultural and forestry practices, particularly overgrazing and its attendant soil degradation and the diminution of the native flora in pastoral country, general disturbance of rangeland and forests, and clear-felling for the woodchip industry, must be causing extinction among invertebrate fauna in Australia. Whether species loss through impact of man provides additional grounds for increased taxonomic effort must be open to debate.

Notwithstanding the social and economic importance of descriptive taxonomy, the CSIRO Division of Entomology, like many similar research institutions in Australia and overseas, encourages its taxonomists to maintain a complementary interest in one or more related fields, perhaps extending the philosophical or theoretical base of classification systems, developing improved methodologies or technologies to assist 'process' taxonomy and higher order classification, or studying evolutionary processes such as speciation and isolating mecha-

nisms, parental investment in rearing offspring, sociality, mimicry, biogeography, co-evolution and so on. This book contains numerous examples of this philosophy in practice, set against a taxonomic framework. Three examples of taxonomic/evolutionary research on insects having an impact upon our understanding of other animal groups are pertinent.

Computer Taxonomy

Electronic storage, processing and retrieval of large volumes of data is ideally suited to the systematisation and analysis of taxonomic information. The DELTA system (Dallwitz 1980; Dallwitz and Paine 1986) was specifically designed for coding taxonomic descriptions of Australian insects, but indeed was first applied to the Australian grasses (Watson and Dallwitz 1985), and thence micro-organisms (Boswell *et al.* 1986). The application of this type of information technology will have a profound influence on both the direction and rate of progress of taxonomic research in the future. It is rewarding to see sophisticated software specifically developed to diminish the 'taxonomic impediment' under which taxonomists, young and old, have laboured, being used in the preparation of this edition of *The Insects of Australia*. However, it remains legitimate to ask whether insect taxonomists are taking adequate advantage of modern information technology to diminish the taxonomic impediment.

Speciation Mechanisms

A conspicuous feature of Australian biology has been the contribution to speciation theory by White, Key and their colleagues. M. J. D. White (1974, 1978) and Key (1974b) first demonstrated that populations of the morabine grasshopper *Vandiemenella viatica* which appeared to be morphologically homogeneous and comprising a single gene pool, were actually divisible into a series of parapatric populations separated by stable but narrow hybrid zones which acted as partial barriers to gene flow. White showed that each population differed by one or more fixed inversion or reciprocal translocations with the result that hybrids in the narrow contact zones were partially sterile or were less viable than individuals from contiguous populations. These zones behaved as genetic 'semi-permeable' membranes permitting some gene flow but acting to accumulate further chromosomal rearrangements so that eventually the original homogeneous population became separated into a series of quite distinct gene pools (Key 1974b). These populations were either lost by subsequent movement of the hybrid zones or were able to enjoy an independent evolutionary future, ultimately as separate species; hence the term coined by White, 'stasipatric speciation'. It was proposed that *Keyacris scurra* and *K. marcida* in N.S.W. speciated by such a sequence of events, as have the *viatica* and $P_{24(XY)}$ forms of *Vandiemenella viatica* on Kangaroo I. (Key 1974b).

The existence of somewhat similar hybrid zones has been identified in other Australian insects, e.g. a phasmatid, *Didymuria violescens* (Craddock 1974), and the grasshopper *Caledia captiva*. Undoubtedly, the latter pro-

vides the best worked and understood example of a chromosome hybrid zone. *C. captiva* has been subjected to detailed chromosomal (Shaw and Coates 1983), electrophoretic (Moran *et al.* 1980), isoenzymic (Colgan 1986) and molecular DNA (Arnold *et al.* 1987) analyses. Shaw and colleagues (1988, 1990) are currently breaking new conceptual ground in biological thinking by demonstrating with *C. captiva* that chromosome morphology can affect cellular and developmental processes, and be subject to strong selection pressure, permitting the evolution of races suited to differing habitats. Clearly their ideas have relevance to karyotype evolution across eukaryotes generally.

Gene pool dissection caused by chromosomal rearrangements has subsequently been shown to be widespread in small mammals (e.g. *Mus musculus* in Italy, lizards in central America and other animals (for review see M. J. D. White 1978)). Thus, using mainly insect data, but acknowledging its generality by reference to a range of vertebrate species, White proposed stasipatric speciation as an important mechanism for animal speciation. By so doing, he explained the intriguing observation that related species often (> 98%) differ in karyotype when their chromosomes are rarely polymorphic (Barton and Hewitt 1981).

Scanning Electron Microscopy

The availability of high resolution scanning electron microscope equipment in the 1960s was first exploited for the description of Australian insects by Taylor and Beaton (1970). The technology was integrated with other procedures concerning publication of type descriptions to overcome the long-standing limitations of traditional, verbal descriptions. The practical and aesthetic benefits of scanning electron microscopy as an illustrative technique in insect taxonomy are outlined in R. W. Taylor (1983). There are beautiful demonstrations of the value of this approach, both for the researcher and the reader, scattered throughout this book; and the general approach is now widely accepted for many groups of insects and other organisms which lend themselves to this mode of description.

Taxonomy and Molecular Biology

Morphological characters have traditionally provided the principal information from which systematists have constructed their classifications. More recently, and to varying degrees, physiological, behavioural, electrophoretic, cytological and chemical analyses have added to the data base of taxonomists. Increasingly, molecular information including amino acid sequencing, DNA-DNA affinity hybridisation, restriction fragment length polymorphism and DNA sequencing have been used to compute genetic distances and construct phylogenies from the sub-specific to the supra-ordinal level and even across phyla (for recent review see Patterson 1987b).

The question of interest, in terms of relative importance of these various approaches, is not whether any one particular approach is under-represented, but rather which approach is most appropriate to the question in hand, and

which questions deserve greatest priority. There can be little doubt that the principal beneficiary of any taxonomist's effort, is a fellow taxonomist, an informed naturalist, or a pure or applied scientist in another discipline such as ecology, biogeography, economic and medical entomology, biological control, environmental sciences, quarantine, and so on. In most of these instances, the user welcomes a practical means of identifying specimens and will be seeking characters whose values are directly measurable by some sensory perception. Such characters are likely to include shape, colour, size, texture, smell, and perhaps habitat, distribution and behaviour. Thus while there continues to be a major taxonomic lacuna in the insect fauna, the primary emphasis must be on descriptive taxonomy using morphological and allied characters, and where practicable, facilitated by modern technologies such as computing and scanning electron microscopy. The virtual absence of catalogues, check lists and diagnostic keys represents a major impediment to the users of insect taxonomy in Australia.

To the non-taxonomist it seems that systematists depend equally on morphological analyses for higher order classification, for resolving problems at the subspecific level and for general descriptive taxonomy. However, the morphological approach appears of less value for either evolutionary extreme and its methods here are often open to ambiguity and subjective interpretation. Fortunately, it is at these levels where the morphological approach falters that certain molecular techniques excel.

For example Avise *et al.* (1983), using DNA restriction fragment length polymorphism within certain mitochondrial genes, investigated successfully the genetic distances and phylogenies of the various species, subspecies and geographic races in the deer-mouse genus *Peromyscus* where morphological techniques had limited resolving power. Similarly, Hillis and Davis (1986), in a detailed study of *Rana*, a genus which dates back over 100 million years and which is morphologically very conservative, also used restriction site mapping of ribosomal genes to determine or confirm monophyly and general phylogenetic relationships in the genus which had not been resolved adequately by resort to morphology alone. Perhaps the most dramatic recent example comes from Sibley and Ahlquist's (1987) analysis of the evolutionary relationships of the Australian songbirds with their relatives elsewhere in the world. On morphological criteria the Australian warblers, flycatchers, nuthatches, creepers etc. had been satisfactorily classified into comparable groups from Europe and Africa. The DNA-DNA hybridisation studies showed, however, that the Australian birds belong to the parvorder Corvida, which has evolved in Australia and New Guinea, and are only distantly related to the European avian fauna which belongs to the parvorder Passerida. This has proved to be an extraordinary example of convergent evolution. According to Sibley and Ahlquist 'Many of the convergences are so subtle that it is doubtful if the true relationship of these groups could have been resolved from anatomical comparisons'. Such examples suggest that we have an ideal situation which

permits complementation between morphological and molecular techniques, the former enabling taxa boundaries to be determined and ready labels to be applied to individual members of a taxon by the users of taxonomy, and the latter providing an accurate picture of the evolutionary record.

A major technical limitation to the use of molecular techniques, especially for DNA sequencing itself, which provides by far the most information on genetic distances, phylogenies and direction of evolutionary change, has been the considerable effort required to isolate, clone and then sequence chosen DNA segments. Fortunately, recent technical advances have diminished many of the obstacles. They involve the recognition by molecular biologists of the enormous information content of certain coding and non-coding DNA sequences in the three ribosomal genes (rDNA) which are represented in multiple copies in all organisms. These sequences can be easily isolated and sequenced directly without cloning because of their abundance and universal distribution (Lane *et al.* 1985). Furthermore, the rate of evolutionary change varies greatly between different rDNA sequences (Appels and Dvorák 1982). Some sequences are highly conserved and these can act as 'universal primers' providing entry into sequences with different rates of evolution. Certain rapidly evolving sequences can be selected for subspecific studies while other conserved sequences permit genetic distance and phylogenetic relationships of phyla to be calculated. Using rDNA analysis, Hori and Osawa (1987) have investigated the origin and evolution of the major groups of organisms, including bacteria, plants and mammals, while Hillis and Davis (1986) have used a similar system for the *Rana* study described above.

It now remains for insect taxonomists to identify the major areas of uncertainty or conflict, preferably in higher order systematics, and to direct the attentions of molecular biologists to these unresolved issues. A comparison of our understanding of the phylogenetic relationships between insect orders in the 1930s (Jeannel 1949) and today (see Kristensen, Chapter 5, Fig. 5.5) suggests that we have become less certain in this area over the past 50 years. A molecular analysis of higher order relationships should prove to be a most profitable exercise. While the molecular techniques are equally powerful at the subspecific level, we should be cautious not to deviate from the principal immediate task of removing the monumental taxonomic impediment, nor allow ourselves to be unduly distracted with subspecific variation and possible speciation events. However, taxonomists must make the effort to understand the extraordinary potential of these new techniques and be prepared to pose intellectual challenges to the molecular biologist who, without such representation, is likely to concentrate on non-taxonomic problems.

Genetics and Cytology and Their Relevance to Evolutionary Theory and Applied Entomology

A conspicuous feature of research on Australian insects, especially in the past three decades, has been in the field of cytogenetics and evolution. This trend was greatly influenced by two leading cyto-geneticists and evolution-

ists, S. Smith-White and M. J. D. White. Through their own endeavours and those of their students and colleagues, we now have clearer insights into a wide range of topics, including: chromosome organisation and behaviour during meiosis and cell division in eukaryotes; chromosomal repatterning resulting in karyotype evolution and speciation, in both insects and vertebrates; sex determination and its evolution; chromosomal polymorphism and genetic systems, including parthenogenesis, in animals.

It is not difficult to demonstrate that the general intellectual climate created by White, Smith-White and colleagues has also had ramifications into applied entomology. Ecological genetics of pesticide resistance and its management (Whitten and McKenzie 1982) and genetic methods of controlling the Australian sheep blowfly, *L. cuprina* (Foster 1980) are two instances.

The studies by Peacock (1970) on chiasma formation in the grasshopper *Goniaea australasiae* and his cytogenetic work on chromosome structure and genome organisation in *D. melanogaster* (Peacock *et al.* 1973) were contributing factors to the foundation of molecular genetics of eukaryotes. It was the combination of Peacock's experience and perspective, together with that of the viral molecular biologist D. Hodgness from Stanford University, which helped initiate the application of molecular genetic techniques first to *D. melanogaster* and then other eukaryotes. Subsequently, the analysis of genome organisation, distribution of non-coding repetitive DNA, eukaryote gene structure and expression, and genetic engineering of *D. melanogaster* have been some of the phenomena explored in hundreds of laboratories across the U.S.A., Europe and Australia in the 1980s. The ability to identify when and in which specific cells particular genes act during development has given unprecedented opportunity to investigate how the biological information, contained in DNA and encoded in other molecules in the insect egg, is drawn upon during embryogenesis and subsequent development. It is thus possible to trace the influence of local studies initiated with Australian insects on the development of this major field of science.

Ecology, Population Dynamics, Biological Control and Conservation Entomology

I have already claimed that entomological science properly began in Australia with Nicholson's 1927 study on mimicry and the conclusions he deduced from the research concerning the regulation of animal populations. Because of the pivotal importance of Nicholson's later research for ecology and its relevance to biological control both in Australia and overseas, we now trace its development in greater detail. Mackerras (1971) summarises the ecological significance of Nicholson's 1927 paper in the following words:

[Nicholson] not only gave a comprehensive review of mimicry and concealing coloration in Australian insects and demonstrated the reality of the phenomena, he also stated the basic principles and hypotheses that he was to spend much of the rest of his life in testing and amplifying. In brief, the thesis he developed was that animal pop-

ulations could not survive in nature unless their densities were governed by some regulatory (feed-back) mechanism that was density-dependent in its operation; that success in searching for essential resources was the only mechanism that was truly density-dependent, all others being merely modifying; that the 'power of discovery' of natural enemies could regulate the abundance of both parasites and hosts; and that natural selection did not determine survival and abundance, it merely ensured that any form of a species that acquired an inheritable advantage, however slight, would progressively replace the previously successful form. In the immediate context, survival and abundance of the mimetic or procrystic insects studied seemed clearly to depend on density-dependent stresses operating on their immature stages, the perfection of their concealment or mimicry on quite minor selective pressures imposed by predators on the adults. The theory was well documented, it gave a credible explanation of the phenomena observed, and it was free from the objections that had been raised against previous theories, some of which, as Nicholson pointed out, were due to failure to understand what Darwin had meant by natural selection.

In the next two years Nicholson attempted to model the regulating influences that predators and parasites have on host abundance, only to conclude that the relationship entailed oscillations of increasing amplitude. Nicholson co-opted a mathematical colleague, V. A. Bailey, who confirmed with mathematical rigour the same conclusions. However, Bailey soon demonstrated that the oscillations became damped when allowance was made for developmental time. These two workers unsuccessfully attempted to publish a book on the 'Balance of Animal Populations' in 1931 which, according to P. A. P. Moran (pers. comm.), contained material and ideas original both to biology and mathematics. They were forced to recast their major findings on host/parasite interactions into a series of papers of which only two major works were eventually published (Nicholson 1933; Nicholson and Bailey 1935).

The largely deductive work of Nicholson and Bailey, arising out of Nicholson's observations on mimetic native insects, had a profound impact on ecological thought in the United Kingdom and the U.S.A. According to Kingsland (1985) the researches of Nicholson and Bailey, along with those of the Canadian ecologist W. P. Thompson and the mathematicians A. J. Lotka and V. Volterra, 'represented the principal lines along which theoretical population ecology developed in the 1920s and 1930s'. G. C. Varley and D. Lack in England are two prominent biologists whose early studies were modelled along Nicholson's line of thinking (Kingsland 1985). H. S. Smith, the pioneering influence for biological control in the U.S.A., and P. DeBach, attempted to provide experimental validation to Nicholson's host/parasite relationships. Indeed, it was DeBach's PhD thesis on house flies and the parasite, *Nasonia vitripennis* (DeBach and Smith 1941) which gave Nicholson encouragement to attempt similar experiments (Kingsland 1985). However, Nicholson had difficulty maintaining a satisfactory culture of the parasite so he decided to study fluctuations in

housefly numbers when parasites were not present. These single species studies were carried out on *L. cuprina* which was more readily available to him than the housefly as an experimental organism. Thus it was more a logistical difficulty rather than some logical necessity that forced Nicholson to 'abandon' host/parasite interactions (temporarily, he thought) for a detailed study of intra-specific competition.

These belated attempts by Nicholson to give experimental respectability to his earlier theoretical, deductive conclusions were rather quixotic. He had become increasingly preoccupied with innate properties of populations. To paraphrase Mackerras's words: Nicholson's population studies are inherently complex and have been bedevilled by criticism and misunderstanding. His basic postulate, from which all his major conclusions follow, and which has been ignored by all his major critics, is simply that no intrinsically variable phenomenon can continue to exist in the absence of a feed-back mechanism to limit its variability. According to Nicholson, 'animal populations are governed fundamentally by processes that are density dependent, all other influences being merely modifying, and the actual population level at any moment being the result of interaction between the governing and modifying processes' (Mackerras 1971). His continued experimentation and published works assisted in fuelling a torrid and largely non-productive debate with his scientific adversaries H. G. Andrewartha at the University of Adelaide, and L. C. Birch at the University of Sydney.

The genesis of this debate can be seen in exchanges of correspondence between Nicholson and J. Davidson, at the University of Adelaide during the early 1930s. Davidson did not endorse Nicholson's concept of self-regulating population forces and argued that climatic factors such as rainfall, evaporation and atmospheric temperature provided an adequate basis for explaining fluctuations in population sizes. These views of Davidson are crystallised in a classic if controversial paper with Andrewartha with supporting evidence from their studies on *Thrips imaginis* (Davidson and Andrewartha 1948). By the time this debate had run its course, many research projects were completed using Australian insects; at least one major teaching text in this field (Andrewartha and Birch 1954) and several other related texts were produced (Browning 1963; Hughes 1974; L. R. Clark *et al.* 1967).

A number of specific studies can be cited which have served as models addressing a wider range of related problems in economic entomology. For example, the findings by Sutherst and colleagues on the factors which influence distribution and abundance of the cattle tick *Boophilus microplus*, and the effects of this ectoparasite on animal health and production, has enabled these researchers to identify a number of management options for reducing considerably the pest status of *B. microplus* (Sutherst *et al.* 1979; Sutherst 1987). These studies have served as a model for developing management options for other ectoparasites around the world.

The studies on tick ecology by Sutherst and colleagues, in recognising the role of climate as a 'major driving variable in the life processes of all ticks', as well as other

invertebrates and even plants, have permitted computer-based predictions of likely distributions of a wide range of organisms, based on climatic information alone (Sutherst and Maywald 1985). CLIMEX, the relevant software package, has been used with considerable success to predict the ultimate pest status of recent accidental introductions of exotic pests into a region, e.g. *Haemaphysalis longicornis* in W.A. (Sutherst pers. comm.), and the medical or economic impact of likely introductions of major pests such as the disease vector, *Aedes albopictus* and the screw-worm *Chrysomya bezziana*. The CLIMEX system is being adopted by applied biologists and increasingly by quarantine authorities around the world (Worner 1988) where there are perceived risks of undesirable plants and arthropod pests entering a country and becoming established. These ramifications all stem from the ecological studies on one model species, the cattle tick, *B. microplus*.

The tick example, illustrating the shift from the particular to the general case, is easy to argue because the influence is already felt and we have the benefit of hindsight. Let us consider an example where the wider ramifications have yet to be realised. The successful control in Papua New Guinea of the aquatic weed *Salvinia molesta* by the weevil, *Cyrtobagous salviniae* (Thomas and Room 1986) provided Room and colleagues an opportunity to model one aspect of insect/plant interaction, namely growth response by *S. molesta* following damage inflicted by feeding *C. salviniae*. Detailed study of plant architecture and developmental responses to the specific feeding damage of the herbivore has wider relevance to economic damage caused to beneficial plants by pest arthropods and to efficacy of weed control by potential biological control agents (Room 1985). The challenge is to derive from the *S. molesta/C. salviniae* model system general principles that can be applied to feeding damage by herbivores in other areas of economic importance.

It is doubtful if the field of insect ecology would have developed as rapidly, or followed the course it did in Australia without the underlying justification of economic entomology and the early successes of biological control of weeds and insect pests. Admittedly, economic entomology has favoured 'single species' studies, where the major pest occupies centre stage, with both the non-biological and biological components of its influencing environment becoming secondary and subservient. Australian examples of this 'single species' paradigm would include, *Lucilia cuprina*, *Dacus tryoni*, *Thrips imaginis*, the bushfly *Musca vetustissima*, *Didymuria viollescens*, the psyllid *Cardiaspina albitextura*, the grasshoppers, *Chortoicetes terminifera* and *Phaulacridium vittatum* and the codling moth *Cydia pomonella* (for literature review see Clark *et al.* 1967; Readshaw 1965; Kitching and Jones 1981). The 'case-study' approach reached its pinnacle in Australia in the 'life systems' methodology as advocated by Clark *et al.* (1967). It was also deployed to great effect by Monro (1967) using *D. tryoni*, *C. pomonella* and *T. imaginis* in his comprehensive classification of the possible relationships between invertebrate consumers and their resources. Monro's insights underpinned

Caughley and Lawton's (1981) analysis of the relationship within and between trophic levels, an analysis which reaches well beyond the invertebrates (Meats 1986).

Undoubtedly, the single species approach was a sound, systematic means for dealing with particular pest species, and certainly was an intelligent way to approach biological and integrated control of specific pests. However, it was applied with less advantage to the control of dung-breeding flies such as *M. vetustissima* and the buffalo fly, *Haematobia exigua*. Although Bornemissza (1960), the original proponent of the importation of exotic dung beetles for controlling dung-breeding flies, always viewed the project as an exercise to readjust ecological perturbation caused by European man, some other biologists have tended to view the program more in the context of classical, biological control focused on *M. vetustissima* and *H. exigua* as the key target pests. In more recent years, the prevailing view has become one requiring a community ecology approach to the problem. Thus, increasing attention has been devoted both to native arthropods which share the dung environment with the pestiferous dipterans, and to the dung itself, in terms of its nutritive quality for flies, beetles and other inhabitants. In overseas studies by CSIRO a similar shift in emphasis has been placed on the community ecology of dung inhabitants. In this way we can hope to detect gaps in the fauna resulting from the relatively species-poor Australian dung community. Emphasis was placed on identifying in the much richer dung communities of Africa and Europe species whose introduction into Australia would have a greater chance of producing a desirable effect, and a lesser chance of generating unintended, unfavourable effects on either the target species, or on the other native inhabitants of dung in Australia. It should also be noted that the change in emphasis from 'single pest species' to community ecology places increasing demands on insect taxonomists and general biologists.

Not only has the economic aspect of entomology shaped the methodology of ecologists and created in them a 'problem orientation', it has also discouraged them from tackling community ecology issues in either natural or disturbed ecosystems. There have been almost no studies of community ecology of native insect groups in undisturbed ecosystems because of the greater difficulty in securing adequate funds for research whose justification is environmental or conservational in nature. However, in future years, there is likely to be increasing recognition in Australia of the economic and cultural significance of the rich and diverse insect fauna. Accordingly, we will need to know more about the importance of insect groups in nutrient cycling, pollination of native plants, habitat creation (e.g. tree cavities caused by termites), and as indicators of environmental pollution, and their importance in maintaining species richness in natural and managed ecosystems. One specific issue requiring greater attention is the possible impact of the exotic honeybee *Apis mellifera* on the native flora and fauna. Are feral colonies having an adverse effect on nectariferous fauna (Pyke and Balzer 1985), and are they changing pollination patterns for native flora as suggested by Paton (1985)?

Consequently, should managed colonies be permitted only restricted access to National Parks and wilderness areas?

Many practising ecologists reflect well the specific requirements of the economic entomologist and are ill at ease when attention is drawn to the need for entomological research in the more nebulous communities of plants and animals that are a major source of the cultural wealth of this isolated continent. In particular, with the mooted changes in continental climate over the next century caused by the greenhouse effect (Pearman 1988) and its probable impact on the flora and general habitats for insects, should we be concentrating more effort on identifying which wilderness areas and their invertebrate fauna are to be earmarked for preservation and study? Probably many such areas are not currently rated as highly as others which are presently resource-rich but doomed by expected climate shifts. If future decades see such a shift in emphasis from economic-based ecology to community and conservation-based ecology there will be an increasing need for insect taxonomists to work in conjunction with ecologists to minimise the obvious taxonomic impediment and to assist in determining research priorities.

Nicholson's 1921–27 study on mimicry remains perhaps the finest example of a natural history study ever carried out in Australia. That analysis played a pivotal role in the development of animal ecology and applied entomology and yet, ironically, it drew Nicholson into a long series of laboratory-cage, simulation studies totally divorced from the natural world. Despite the increasing need for research in economic entomology over the 1990s, the demands of the 21st century are likely to be for a community ecology approach to disturbed, managed and natural ecosystems. We need to consider more carefully the philosophy and methodology advocated by Nicholson in 1927.

Neurobiology, Development, Behaviour and Medical Science

It is not surprising that insects have featured as fruitful models in such classical disciplines of taxonomy, evolution, ecology and cytogenetics; nor is it particularly surprising that many of the principles of cellular biology and intermediate metabolism have been developed using insect models. However, it was not expected that insect models would prove so critical to modern investigations in the fields of neurobiology, development, vision, behaviour (including learning and short and long term memory), nor in studying genes whose malfunction in humans is responsible for illness or disease in their carriers. Let us consider several recent examples from molecular genetics. What these examples have in common is that they demonstrate the existence of genes in invertebrates which are key regulators of differentiation and development or which control central metabolic processes concerned with neurological functions or behaviour, and they show strong homologies with genes in vertebrates including man.

Such a critical role for invertebrates as model organ-

isms for studying development was actually foreshadowed by Bateson (1894) who predicted that an understanding of homoeotic variation (the development of an organ where another normally develops e.g. antenna-pedia) might provide a clue to the ground rules governing ontogenetic and phylogenetic change. Bateson's insight has been given substance with the recent discovery by McGinnis *et al.* (1984) of the existence of a homologous protein-coding sequence of about 180 nucleotide bases in a group of genes in *D. melanogaster* whose malfunction causes the development of homoeotic variants. This sequence, termed a homoeobox, is conserved in other metazoans including annelids, frogs, birds, mice and man (Struhl 1984). Saint *et al.* (1988) have demonstrated with studies on the *rough* gene in *D. melanogaster* that homoeobox-containing genes can also influence tissue differentiation in imaginal discs (clusters of undifferentiated cells which persist in larvae and pupae and give rise to adult organs); thus the influence of these genes is not restricted to early embryological events. Other ubiquitous sequences that code for proteins which bind to DNA or RNA have been first identified either in *D. melanogaster* or the frog, *Xenopus*. One such example is the class of 'zinc finger' proteins, so called because of a particular repeated structural motif which enables the protein to bind to specific DNA or RNA sequences. Such structures occur in 'many regulatory proteins and serve as modules for the building up of a specific nucleic acid binding domain' (Klug and Rhodes 1987). Genes containing such elements, e.g. *Kruppel* and *hunchback* in *D. melanogaster*, are emerging as key regulators of segmentation and other early developmental events.

Although the particulars of embryogenesis are quite different in invertebrates and vertebrates, some of the central principles regulating differentiation appear as if they may well apply to most metazoans (Nagorcka 1988, 1989). The extensive knowledge of genetics and embryology of *D. melanogaster* and other insects, together with the reasons outlined earlier in this chapter on the general suitability of insects as model experimental organisms, puts such insects in a very privileged position for generating fundamental knowledge of animal development.

Bateson (1894) also recognised that homoeotic variation may have a bearing on morphological discontinuity between species. He stated: 'The first question that the study of variation may be expected to answer relates to the origin of that discontinuity of which species is the objective expression. Such discontinuity is not in the environment, may it not then, be in the living thing itself?' Garcia-Bellido (1977) has addressed this issue and suggests that homoeotic and atavistic mutations in insects are functionally related and can give a clearer indication of the specific steps leading to discrete morphological differences between taxa of varying evolutionary relatedness.

It is now recognised that the high degree of conservation of DNA sequences allows DNA segments from vertebrates to act as probes for screening DNA libraries from invertebrates for homologous sequences, or vice versa. Cowman *et al.* (1986) isolated two opsin-coding genes

from *D. melanogaster* using a bovine opsin gene as a probe. Similarly Walker *et al.* (1986) isolated the gene which codes for tryptophan oxygenase in *D. melanogaster* using the homologous gene from rat liver as a probe. Analysis of gene function and evolutionary divergence across a wide range of plants and animals provides the scientist with an extraordinarily powerful set of tools.

Miller and Benzer (1983) have shown that around 50% of 146 monoclonal antibodies specific for proteins taken from *D. melanogaster* head, brain or retina showed immunofluorescent staining in one or more human nervous system sites. These results suggest 'the possibility of evolutionary conservation of many more central nervous system molecules than hitherto known' (Miller and Benzer 1983). The authors conclude: 'Many human neurobiological defects are hereditary, but progress in human disease has been stymied often by the lack of model systems. *Drosophila* mutants also display hereditary pathologies such as brain degeneration and muscle defects resembling nemaline myopathy [a muscle disorder in humans]. With currently available recombinant DNA technology, it may well be feasible to transfer a selected gene from human to fly in order to study its function'.

In a similar vein, Goodman and Bastiani (1984) in addressing the questions of how embryonic nerve cells recognise one another during development stated:

How are neuronal growth cones guided to their targets in a developing embryo? To what extent can growth cones and filopodia specifically recognise the surfaces of other neurons during development, and to what degree are those surfaces differently labelled? What is the molecular code of the surface labels and how is it deciphered by developing growth cones? To answer such questions many of us who hope someday to understand how the human brain is wired during development have begun by studying the far simpler brains of invertebrate animals.

In reaching such conclusions, Goodman and his colleagues are investigating neuronal specificity in the embryos of two insects: the grasshopper *Schistocerca americana* and the fly *D. melanogaster*.

A powerful tool of genetic analysis is to generate mutations which affect biochemical pathways. By studying the effects of these specific lesions, it is possible to build a comprehensive picture of how the systems function normally. For example Summers *et al.* (1982) used eye colour mutations in the sheep blowfly *L. cuprina* to identify the specific enzyme steps which regulate tryptophan conversion into the ommochrome pigment that is essential for vision. These blowfly studies were modelled on Beadle and Ephrussi's (1937) investigation of eye pigments in *D. melanogaster*. This same *D. melanogaster* work triggered Beadle and Tatum's (1941) intensive investigations of biochemical mutations in the mould, *Neurospora*. The significance of the *Neurospora* studies was encapsulated in the 'one gene-one enzyme' principle, attracting the Nobel prize for its authors.

Similar techniques have been used to isolate *D. melanogaster* mutations which prevent their carrier from learning or remembering normally. Some of these muta-

tions influence synthesis of cyclic-AMP, others affect its degradation, while other mutations influence the levels of monoamines (for review, see Dudai 1985). It is recognised from invertebrate studies (*Drosophila*; the molluscs, *Aplysia*, *Hermissenda*) that short-term memory involves modification of pre-existing proteins without *de novo* gene action, while gene expression is required before the information is committed to long-term memory (Goelet *et al.* 1986; Willmund *et al.* 1986).

As Dudai (1985) states, such studies are designed 'to reduce memory to a sub-cellular and molecular language'. Another related example comes from the work of Schwarz *et al.* (1988) which has established that the wide diversity of potassium channels critical to the control of the excitability of nerve and muscle result, at least in part, from alternative splicing of the transcript from a single gene at the *Shaker* locus in *D. melanogaster*. Timpe *et al.* (1988), using the *Xenopus* oocyte as a medium for gene expression, provided evidence that a single *D. melanogaster* *Shaker* messenger RNA species, presumably derived from specific splicing of the primary transcript, codes for 'A' type channels, or one of its sub-units, in *Xenopus*. Because of the probable common ancestry of the invertebrate and vertebrate nervous systems, it clearly is more practical, first to dissect the components of structure, function and ontogeny in *D. melanogaster* and other relatively simple invertebrate models and then to devise ways to validate extrapolation to other animals including humans.

One final example of the potential importance of insect research to human health comes from studies on the relationship between genes, development and cancer. Gateff (1982) developed the case for the causal linkages between these three levels largely using evidence from *D. melanogaster*; and certainly *D. melanogaster* promises to be a central model in further exploration of the molecular genetic basis of malignant neoplastic transformation.

These examples are not intended to suggest that neurological processes such as learning and memory in humans and *Drosophila* are identical. Rather, we are confident that the superb experimental system presented by *Drosophila* and other insect models will assist in our asking more pertinent questions and tackling them more effectively when we approach the more complex and refractory *Homo sapiens*. We could be even more confident that the insect model system will help us understand better the causes of some genetically based defects in some human behaviour (Dudai 1985).

As stated earlier the choice of model systems for studying basic biological and biomedical phenomena can be traced to Owen in 1843 (Scharer 1987). For over a century this choice has been justified by the relatedness of organ structures because of their common evolutionary ancestry. Scharer (1987) has pointed out that models based simply on homology ignore the value of 'the functional correspondence of analogous biological systems', and therefore are unnecessarily restrictive. She proceeds to show how our current understanding of the integrative control of the body's various behavioural and developmental functions by the neuroendocrine apparatus derives

equally from studies of invertebrate and vertebrate models. Scharer's comparative analysis of the neural and endocrine systems of invertebrates and vertebrates demonstrates 'remarkable structural and functional parallels between the two animal phyla'. If the invertebrate model provides insights into how the vertebrate system might function, or vice versa, then the question of common ancestry is of less relevance.

The use of insect models for medical research, in Australia at least, is unlikely to reach its full potential until medical researchers and funding agencies accept their legitimacy in this role. Increasing recognition by biomedical scientists in North America of the principle of analogy in model systems can be seen in Anon. (1985). Traditional medical thinking in Australia has tended to limit model animals to sheep, mice and cats. There is even reluctance to accept marsupial models which offer enormous benefits for studies in developmental biology and reproductive physiology because of the undeveloped status of accessible pouch young (C. H. Tyndale-Biscoe pers. comm). Consequently, we have much progress to make before the predictions of Goodman, Miller and Benzer are likely to become a reality in Australia.

The Integration Between New and Old Technologies, and the Role for Insects

It would be wrong to suppose that the phenomenon of learning in insects was discovered by molecular biologists and neurobiologists working with *D. melanogaster*. As in other cases, these newer methodologies can only be adequately exploited when based on a long tradition of scholarly application of more classical methods. For example, evidence of learning in arthropods dates back to an 1887 paper by E. G. Peckham and G. W. Peckham on habituation in spiders (see Thorpe 1956). Studies on conditioning of vertebrates by E. L. Thorndyke and I. P. Pavlov earlier this century probably influenced similar studies on associative learning in mayfly nymphs and cockroaches (see Thorpe 1956). Later K. von Frisch and a large cohort of students demonstrated the honeybee's ability to utilise experiential information for more effective foraging. While this latter knowledge had little impact on practical beekeeping it indicated that invertebrate sensory receptors and their central nervous system provided the Insecta with a capacity for learning. It also showed how long and short term memory could be used in survival. More recently, Traynier (1986 and unpublished) has demonstrated the importance and plasticity of visual learning and olfaction in determining the discrimination power of foraging or gravid, phytophagous insects. Such background knowledge becomes essential to the molecular geneticist who is forced to use insects such as *D. melanogaster* which are genetically well understood but for which there is not a long tradition of research on topics such as learning and behaviour.

Insect model systems have not always led the quest for new knowledge. For example, the existence of a class of small peptides which influence the transmission of sensory information through the nervous system was well

established in vertebrates before the same class of peptides was recognised in insects. Scheller *et al.* (1983) demonstrated in the marine mollusc *Aplysia* that a single gene codes for one precursor protein which is then cleaved into 11 smaller peptides. These then act in concert on specific, identifiable neurons resulting in co-ordination of the actions surrounding egg laying. Such studies stimulated the search for similar acting peptides in insects, which regulate physiology and behaviour. For example, Tublitz *et al.* (1986) have shown that three inter-related peptidergic systems coordinate behaviour concerned with eclosion in the tobacco hawkmoth, *Manduca sexta*. O'Shea (1985) has reviewed the role of neuropeptides in insect behaviour and predicts that a large number of different neuropeptides exist in insects and that these contribute to the regulation of fixed-action patterns of behaviour.

Insect Models and Information Technology

It is surprising to discover that the ways in which insects visualise objects in a three-dimensional world can suggest solutions to refractory problems in the high-technology world. Just two examples arising from fundamental studies of insect vision will suffice. Snyder (1979), studying polarisation of light before it entered and traversed the 7th rhabdomere in the ommatidium of the housefly *Musca domestica* and the relevance of polarisation to energy loss in the rhabdomere, realised that knowledge of this system could be used to improve the transmission efficiency of light energy along optical fibres by some 100-fold. He also recognised the relevance of the rhabdomere model for the design of an artificial light guide, resulting in the construction of low energy sensors for security and medical detection systems. Both applications have vast potential for information technology (G. A. Horridge pers. comm.)

In another area, Horridge (1987) has shown the inappropriateness of higher animals visual systems as models for developing artificial vision systems for use in robotics. 'Seeing' in higher animals is more a memory-related process than a direct three-dimension construction following processing of sensory inputs. Consequently, artificial vision using video cameras requires processing by an enormous memory bank before the robot can 'see' an object in three-dimensional space. Horridge has reviewed the wide range of visual systems that exist in the animal kingdom in terms of their suitability as models in robotics. He has postulated that the insect system which allows an individual to 'see' stationary objects while moving itself, through 'error of parallax', does not involve significant memory and therefore its artificial analogue should not demand a massive electronic memory equivalent. Several groups are now working towards practical, artificial vision systems based on the insect model as interpreted by Horridge. No doubt other 'invertebrate solutions' will continue to provide inspiration to modern industrial technologists.

It is interesting to note that insect vision has been shown to be a valuable model in both analogous mode (i.e. comparing the process of seeing through the com-

pound eye of the invertebrate and the simple eye of the vertebrate) and in homologous mode (i.e. the opsin genes of invertebrates and vertebrates whose common sequences presumably indicate a common ancestry).

Will Australian Insects Play a Unique Role in the Biological Sciences of the 21st Century?

From what has already been advocated about 'universal truths' being revealed through the use of model insects, it would be inconsistent and naïve to suppose that Australian insects will contribute to the broad body of scientific knowledge in some unique manner not possible though a study of exotic species either in local laboratory experiments or in their natural habitats overseas. What makes the pursuit of basic, biological science feasible is the belief that there is a finite number of processes, principles and mechanisms governing evolutionary and developmental change and determining the way in which an organism can respond to exogenous or endogenous signals. Furthermore, the number of biological solutions to evolutionary problems appears to be finite, albeit large in the case of insects. This last point has already been well illustrated earlier in this chapter with the convergent evolution of the Australian bird fauna and their European counterparts. For over a century the various Australian songbirds were erroneously grouped with their morphological equivalents in the European bird fauna but have now been shown to have evolved endemically from founding stock over the past 55 million years (Sibley and Ahlquist 1987). This and many other examples of parallel and convergent evolution, tend to suggest that a finite number of biological solutions is possible once a general 'body plan' has been 'adopted' by one's ancestors. In other words, in any study using Australian insects as models, the particulars may show interesting variation in detail, but the broad principles and underlying mechanisms are likely to be universally applicable.

What remains of interest, then, is how and to what extent biologists have used, and will continue to use Australian subjects to confirm and extend a discovery or a theory first enunciated overseas; or indeed where biologists in Australia have exploited local material to establish *de novo* some principle or process which is subsequently accepted widely or confirmed by overseas studies. Space does not permit the discussion, in any detail, of a large number of cases where Australian insect material has been used to identify principles, or to confirm or extend what has been discovered elsewhere but a listing of such examples, not otherwise referred to in this chapter, would include:

P. A. Parsons and I. Bock's studies on the degree of speciation of the Australian Drosophilidae and its relevance to colonising theory (Parsons and Bock 1981); Brundin's (1966) biogeographic interpretation of the Southern Hemisphere Chironomidae in the context of continental drift and cladistic theory; C. N. Smithers and I. W. B. Thornton's biogeographic studies on the Psocoptera (Smithers, Chapter 28 this book; Thornton 1985); and D. T. Gwynne's perceptive studies on the role of parental investment in determining sexual behaviour in

katydid. The opportunity to study species such as the katydid, *Metaballus litus*, in which male investment varies between populations from a simple sperm transfer to the provision of a nutritious spermatophylax weighing up to 40% of the male body weight, provided Gwynne and colleagues with a unique and magnificent opportunity to study the evolutionary plasticity of parental investment (Gwynne 1985). Other examples of valuable Australian studies would include those of the variable sex-determining systems in *M. domestica* where the XY chromosomal system has been replaced since the introduction of the pesticide DDT by two successive autosomal particulate systems controlling sex determination (Kerr 1970; Wagoner *et al.* 1974); and studies of parthenogenicity in several orthopteran families and its putative hybrid origin (White *et al.* 1977); the role of auditory genes in male bushcrickets for territorial spacing and calling females (Römer and Bailey 1986). Martin and colleagues have studied particulate sex determination in chironomids and have demonstrated mobility of the maleness element (Martin and Lee 1984). These workers have cloned the relevant DNA segment and their preliminary results suggest the existence of a highly conserved sequence which controls sex determination (Martin pers. comm.). Naturally occurring pheromones have been used in the taxonomy of Australian tortricids and in studies of pre-mating isolation in these moths (Horak *et al.* 1988). Synthetic pheromones have been used to monitor populations or disrupt mating in economically important Lepidoptera (Vickers and Rothschild 1985). Gene introgression between *Dacus tryoni* and *D. neohumeralis* was widely proposed by Lewontin and Birch (1966) as a general means of enabling ecological expansion of an insect population but Vogt (1977) in a less well-known study demonstrated that the example was not well founded. The recent discovery by Fitt (1989) that the distribution and host plants of native dacines are determined more by innate host plant preferences than by competitive exclusion dispels another long-held myth. Observations of communal, pre-social wasps and bees sustain debate on the origins of social behaviour (e.g. Evans and Hook

1986), and Crozier and colleagues have contributed to the theory of kin selection using social hymenopterans as model species (Crozier 1987).

Australian scientists undoubtedly will continue to use particular native or cosmopolitan insects as models in advancing knowledge on a wide range of topics of economic or scientific importance to humankind. However, perhaps the most important contribution Australian entomologists can make to the cultural and economic betterment of humanity will follow from a more convincing demonstration that biological diversity is essential to the cultural wealth of modern societies. Already humans consume directly or indirectly over one third of total, terrestrial, photosynthetic productivity, and the greater proportion of the consumption is in the tropical zone where species diversity is maximal (P. H. Raven 1986; Wilson 1985d). Australia is one of the few developed countries in the world with a significant tropical flora and fauna. While its tropical regions are not currently subject to intense human pressure there are mounting demands to extend agricultural activities into the area, and tourism is a strong growth industry. Future generations might well be grateful that the threat of damage by native and exotic insects to agricultural plants and livestock is a major factor in stemming rural development in Australia's Tropics. We might conclude that Australian entomologists have a special responsibility to exploit this 'insect driven' impediment to development by finding ways to study the extensive native insect fauna in tropical Australia as a model system. An understanding of this still, near-pristine system could give greater legitimacy to the claims by Wilson (1985d) and Raven (1986) that man's continued survival is irrelevant without an accompanying species diversity.

Australia as a developed nation has an obligation to set an example in vegetation and faunal conservation to developing nations, who are contributing so heavily to the greenhouse effect and land degradation. Our endeavours to set such an example will be meaningful only if we make the study of native invertebrate fauna a pivotal item in our scientific agenda.

Collembola

(Springtails)

PENELOPE J. GREENSLADE

Small to minute, pigmented or white wingless hexapods; mouth-parts entognathous consisting of elongate maxilla and mandible enclosed by folds of plica oralis, labrum and labium; postantennal organ primitively present, maximum of 8 + 8 ocelli; antennae 4-segmented, with intrinsic muscles in all segments, sometimes subsegmented; thorax with 3 segments, 1st segment reduced; legs basically 4-segmented; abdomen 6-segmented with specialised appendages ventrally on 1, 3 and 4, genital opening on 5; cerci absent but anal spines sometimes present. Instar development is gradual (ametabolous or epimetabolic).

Springtails are soft-bodied arthropods. Adults are usually 1–3 mm long, but a few can reach 10 mm. A variety of life-forms are represented (Figs 11.5–8). Many species are white or black or various shades of grey but others are coloured and patterned. Collembola are furnished with setae which can be numerous or sparse, fine or thick, long or short, serrated, ciliated, clavate or smooth. Scales and *bothriotricha* (long, usually ciliated, slender setae inserted in a pit) are found in some families. World-wide over 6000 collembolan species in about 500 genera have been described. There may be nearly 2000 species in Australia, many undescribed, making it the seventh largest order included in this volume. The common name, 'springtail', is derived from the ability of many species to leap considerable distances when disturbed. For general accounts of the group see Schaller (1970) and Massoud (1971a), and for accounts of their biology, see Christiansen (1964), Joosse (1981, 1983), Fjellberg (1985a) and Joosse and Verhoef (1987). The literature was indexed by Salmon (1964) and the Australian species reviewed by Womersley (1939) and Greenslade (in press).

It has been suggested on embryological and morphological grounds that the relationships of the Entognatha (Collembola, Protura and Diplura) lie with the myriapods

and in particular the Symphyla (Gupta 1979), but this hypothesis has been disputed (Manton 1972). According to Hennig (1981) the sister group of the Collembola is the Protura.

Anatomy of Adult

Head (Figs 11.1A, B). Primitively prognathous, but more or less hypognathous in the Symphypleona and Neelipleona. Antennae with 4 segments which can be subdivided into 2 (antennal segments 1 and 2) or numerous (antennal segments 3 and 4) subsegments, and varying in length from shorter than head to longer than body; antennae sometimes modified in male as clasping organs (Fig. 11.1C). All segments carry some parallel-sided, thin-walled chemosensory setae (sensilla) as well as normal setae which are most dense distally on antenna 4 where the apical glandular lobe is positioned in Poduroidea. Antennae 3 almost always with a laterodistal sensory organ consisting of at least 2 sensilla and 2 guard setae (Fig. 11.3D). A *postantennal organ* which has an olfactory function is usually present, varying in form from a simple, circular structure (Fig. 11.3F), to a multituberculate sensory area (Figs 11.3A, B). Pairs of pseudocelli (circular areas of thin, corrugated cuticle) are distributed on the

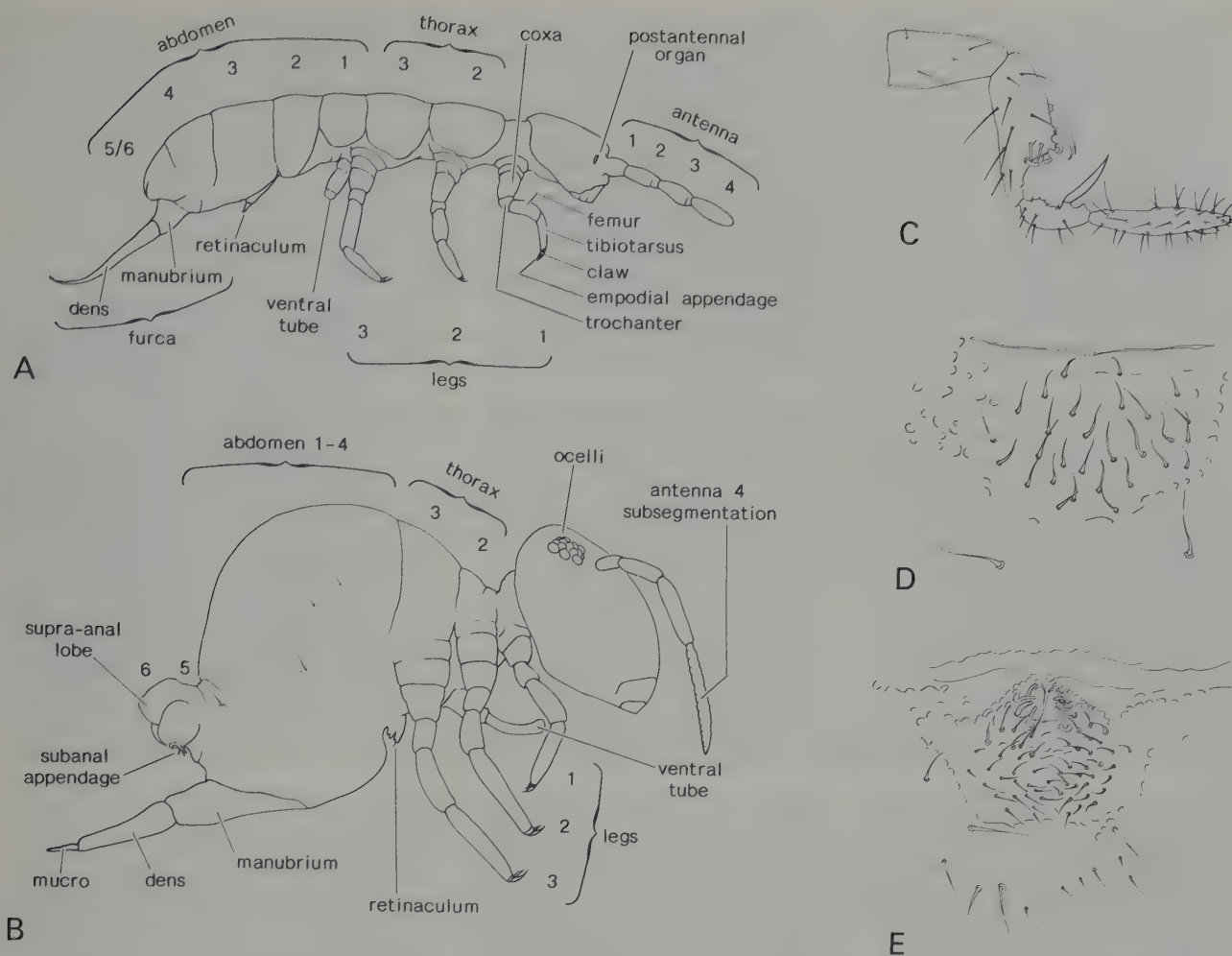


Fig. 11.1 External morphology of Collembola: A, *Folsomotoma* sp., Isotomidae; B, *Katianna* sp., Sminthuridae; C, *Jeannenotia violacea*, Sminthuridae, ♂ antenna; D, *Friesea tilbrookii*, Neanuridae, ♀ genital opening; E, *F. tilbrookii*, ♂ genital opening. [A, B by J. Thurmer; D, E from Greenslade 1986b]

head and body segments of Onychiuridae (Fig. 11.3E). There is a maximum of 8 + 8 ocelli on a pigmented patch on each side (Fig. 11.3F). Mouth-parts (Fig. 11.2) elongate and protrusible, adapted either for biting and chewing/grinding, or for fluid feeding; mandible occasionally absent, when present with single condyle and often with finely toothed lateral (molar) plate (Fig. 11.2A), mandibular head nearly always with teeth (Figs 11.2B, G); maxilla with a maximum of 6 fringed lamellae with 3-toothed *ungulum* and pair of posterior extensions (*fulcrum*) on which cardo articulates. Supported on the fulcrum there is an apparent tentorium to which the muscles of the head and mouth-parts are attached. Hypopharynx well developed, trilobed, with superlinguae flat, immobile, plate-like. The submentum reduced by encroachment of cranial folds and the labium connected to clypeus through *plica oralis* (pleural folds) which together with labrum and labium completely enclose other mouth-parts and project anteriorly to form the buccal cone; labial and maxillary palps rarely well developed, sometimes reduced or absent.

Thorax. Segments are clearly distinguishable in

Arthropleona but not in Symphypleona or Neelipleona; thorax 1 reduced or vestigial. In Symphypleona and Neelipleona thorax fused to abdomen. Each leg divided into 2 superficial subcoxae, coxa, trochanter, femur and tibiotarsus. A trochanteral or coxal organ is sometimes present (Fig. 11.3C) and consists of a single spine or a field of short, regularly arranged setae. The tibiotarsus often bears at least one long tenent hair, frequently clavate and producing a secretion from a basal gland. Pretarsus nearly always with external and internal setulae; bears single claw (Fig. 11.3H) (*unguis*) often with internal, lateral (*pseudonychia*) and external teeth and occasionally with sheath-like tunica. Empodial appendage (*unguiculus*), when present, setose and usually with at least one lamella, which can be toothed.

Abdomen. Six-segmented: segments 1–4 form the pre-genital region, segment 1 ventrally carries the *ventral tube*, 3 the *retinaculum* and 4 the *furca* (*furcula*) or spring. The ventral tube consists of a basal column with a pair of smooth-walled, apical diverticula which are normally retracted within the base but which can be extruded by hydrostatic pressure. The ventral tube is connected to

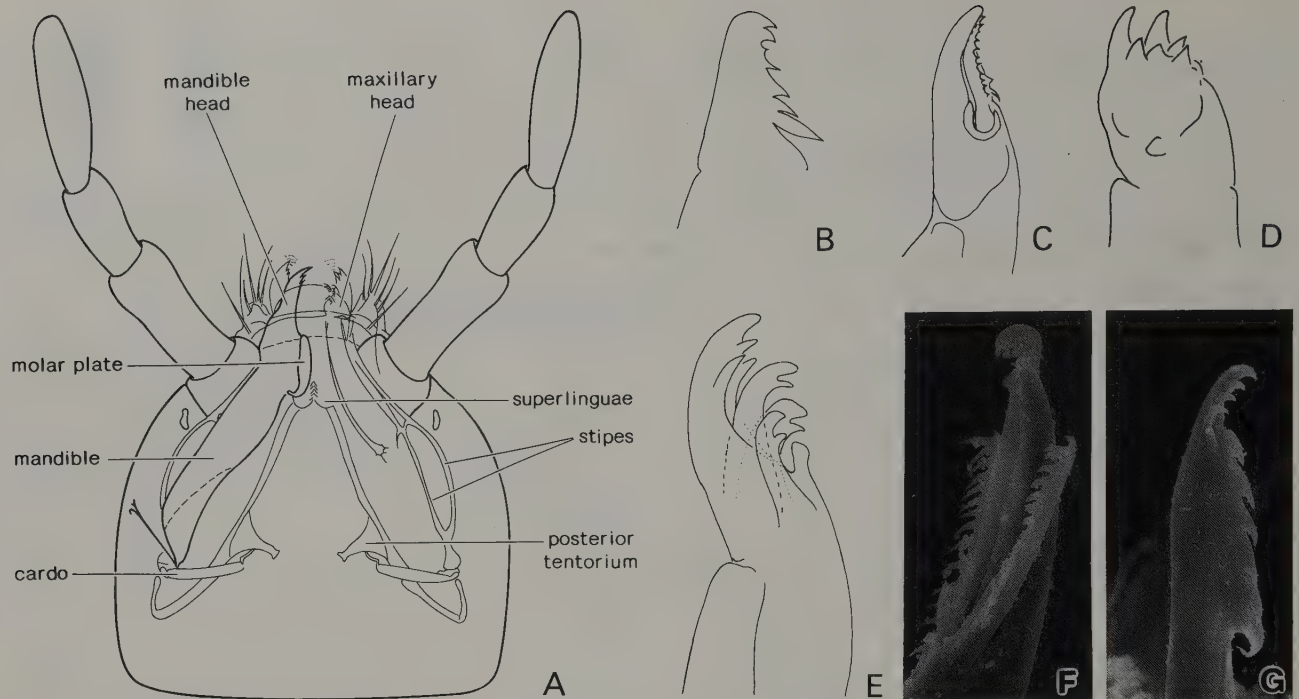


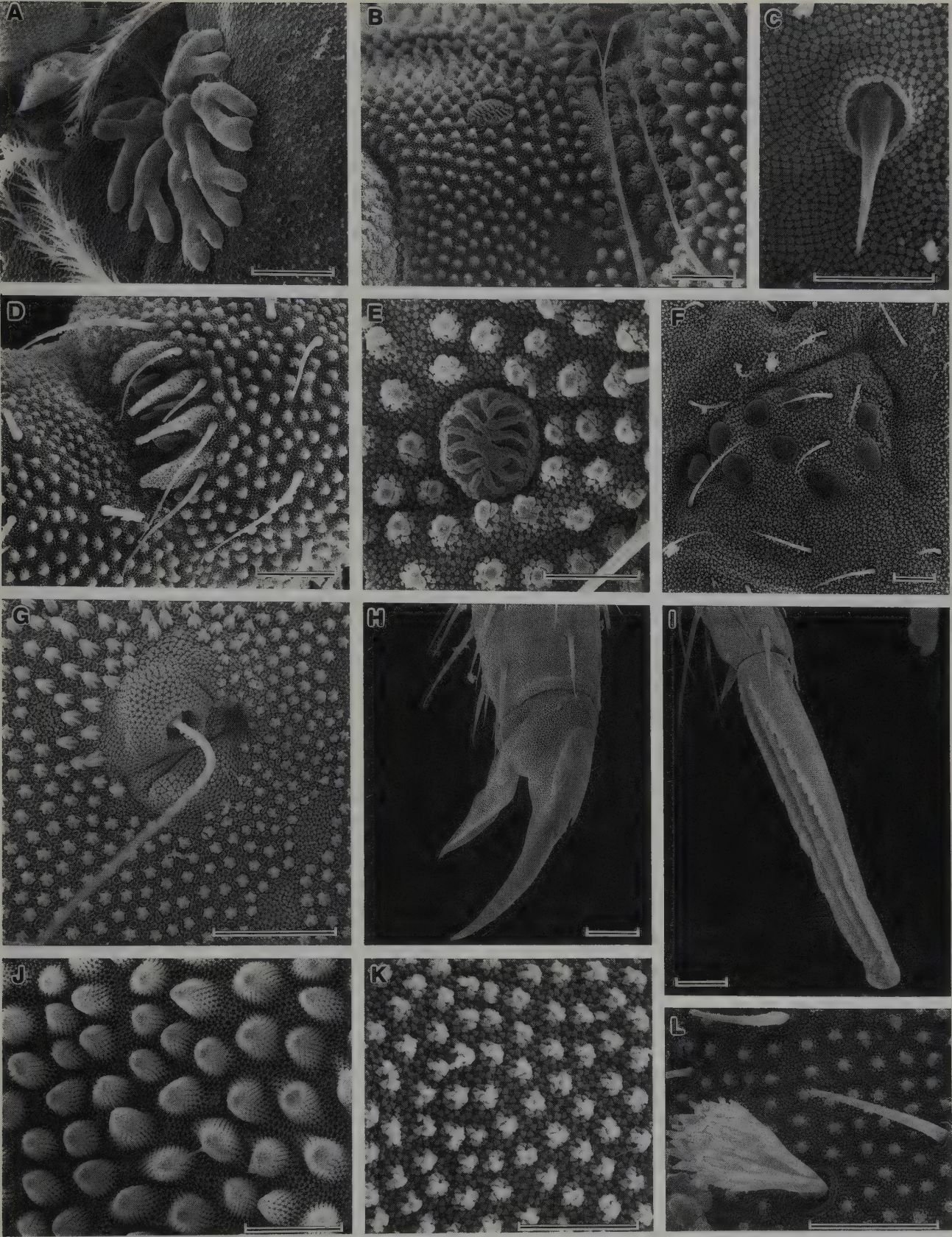
Fig. 11.2 Mouth-parts: A, *Folsomia candida*, Isotomidae; B, *Friesea tilbrookii*, Neanuridae, mandible; C, *F. tilbrookii*, maxilla; D, *Brachystomella diana*, Brachystomellidae, maxilla; E, *Salvarella wallacei*, Brachystomellidae, maxilla; F, *Pseudachorudina* sp., Neanuridae, maxilla; G, *Pseudachorudina* sp., mandible. [A after Goto 1972; B, C from Greenslade 1986b; D, E from Greenslade and Najt 1987b, a; F, G by K. Pickerd]

the external aperture of the labial glands (or nephridia) on the head by a ventral groove, which is an open, partially closed or completely closed tube; it acts as a coelomoduct carrying uric acid from the nephridia to the ventral tube by capillary action. The function of the ventral tube was thought to be adhesive (hence Collembola, *Colle*—glue, *embolon*—piston (Greek)) and in some sminthurids it does secure the animal after leaping. Another function of the ventral tube is osmoregulation and it is filled with haemolymph when extruded. Its epithelium plays a part in ion and water transport, excretion and respiration, and it appears to provide lubrication to the legs for grooming. The furca consists of a basal part, the *manubrium* and a pair of *dentes* (sing., *dens*) attached distally, terminating in toothed, spined or lamellate *mucrones* (sing., *mucro*; Fig. 11.3i). Normally the furca is flexed forward beneath the body and held in place by the teeth of the retinaculum. When suddenly released by muscular pressure, the furca returns to the unflexed position hitting the substrate and forcing the animal into the air. Acceleration varies from $120\text{--}970\text{ ms}^{-2}$ according to family and the energy required is $10^{-9}\text{--}10^{-7}\text{ J}$ with a take off velocity of 1.4 ms^{-1} (Christian 1979). The Sminthuridae are the most active, leaping vertically 30 cm or more at high speed while the Entomobryidae leap more slowly and horizontally. In

Entomobryidae and Sminthuridae a click mechanism is involved to return the furca to its flexed position. Jumping is both a phobic reaction and a means of dispersal and can be induced by air currents. The genital aperture on abdomen 5 is a horizontal setose slit in the female and a raised and densely setose vertical slit in the male (Figs 11.1D, E). Anal aperture on abdomen 6 encircled by dorsal (supra-anal) lobe and a pair of ventral anal lobes. Cerci absent but anal spines may be present; often there are 2 spines but up to 10 can be found. Most sminthurid females have a pair of subanal appendages.

The cuticle is ornamented primitively with triangular primary tubercles which are arranged in hexagonal rosettes and connected by three ridges arising from their sides. The tubercles and their connections can be fused, enlarged or raised to form secondary and tertiary tubercles, digitations or bosses in patterns generally characteristic of each family and related both to phylogenetic position and to the humidity of the habitat in which the species lives (Figs 11.3J–L). Cuticular tubercles are covered with wax but spaces between are usually bare and canals connected with the interior have their openings there. Primitive hypothetical chaetotaxy consists of 3 rows each of 7+7 setae per segment and evolutionary trends have been towards either reduction, multiplication

Fig. 11.3 A, *Oncopodura* sp., Oncopoduridae, postantennal organ; B, *Onychiurus* sp., Onychiuridae, postantennal organ; C, *Katianna* sp., Sminthuridae, trochanteral organ; D, *Onychiurus* sp., antenna 3 organ; E, *Onychiurus* sp., pseudocellus; F, *Gomphiocephalus hodgsoni*, Hypogastruridae, ocelli patch and postantennal organ; G, *Adelphoderia regina*, Sminthuridae, bothriotricha; H, *Folsomotoma bioculata*, Isotomidae, claw; I, *A. regina*, mucro; J, Neanuridae–Uchidanurinae, cuticle; K, Sminthuridae–Katianninae, cuticle; L, *Neosminthurus*, Sminthuridae, cuticle. Scales: A, C, E, K = 5 μm ; B, D, F–J, L = 10 μm . [C. Beaton, K. Pickerd]



or diversification of setae and scales. Body segments always with parallel-sided, thin-walled sensory setae and often with bothriotricha (Fig. 11.3G).

Internal Anatomy. Head with pair of labial glands (nephridia) ventrally and 4 pairs of salivary glands dorsally. In Neanurinae some of the latter may have polytene chromosomes ($2n = 8-14$). Alimentary canal generally a simple tube with short fore gut, large mid gut and small hind gut; Malpighian tubules absent but Malpighian papillae present. Cardiac valve not well developed but there is a complex pyloric sphincter with ring cells. Peritrophic membrane present. Dorsal blood vessel extends to abdomen 4, and has 2-6 ostia. Nervous system with supra- and sub-oesophageal ganglia and 3 ventral ganglia; abdominal ganglia fused to 3rd thoracic ganglion. Neurosecretory and retrocerebral systems similar to those of insects with corpora cardiaca and corpora allata. Excretion performed partly by labial glands via the ventral groove, partly through loss of excretory concretions in mid gut epithelium during ecdysis and, in several families including Sminthuridae, by fat bodies which accumulate urates. A few Sminthuridae (Sminthurinae) and Actaletidae possess a pair of ventral spiracular openings between the head and thorax with a system of ramifying tracheae throughout the head alone or head and body. However in most Collembola respiration is cutaneous and by means of the ventral tube (see above). For the same biomass, a collembolan with tracheae requires twice the oxygen of one without tracheae. Reproductive organs consist of paired ovaries or testes with single duct leading to genital aperture; female with pair of small spermathecae; male of some species with complex, sclerotised ejaculatory apparatus. The muscular system of *Tomocerus* is described by Manton (1972).

Immature Stages

The eggs are spherical, pale, and have a smooth or finely sculptured chorion, which ruptures early. Segmentation is initially complete; there is no amnion (foetal envelope) but the embryo has a well developed dorsal organ present vestigially in the 1st instar of a few species. Apart from the 1st instar, the juvenile resembles the adult and is often difficult to distinguish either on size or on morphology, although complete adult chaetotaxy and colour gradually develop during the pre-adult instars. The chaetotaxy of the 1st instar constitutes the primary chaetotaxy while that of the later stages is described as the postembryonic or secondary neochaetotaxy. Differences seen between 1st and 2nd instars are insufficient to be classified as metamorphosis, although in the Entomobryidae, the 1st instar lacks scales and in the Symphypleona it has an unmodified cuticle, reduced tracheal system and less control over water loss than the adult. There are normally five to ten ecdyses before maturity, and egg to adult on average takes two to three months, but this varies greatly with taxon and temperature. Development can take over two years in *Tetradontophora* or only a week in *Sphaeridia*. Adults continue moulting throughout life, and may undergo up to 50 moults in some species, although no further increase in size usually occurs after about moult 15.

Biology

Reproduction. Sperm transfer is indirect, the males depositing on the ground a globular, stalked spermatophore in which sperms with $9 + 2$ flagellar elements are encysted. Mating behaviour that ensures females find and take sperm into the genital aperture varies. In Hypogastruridae and some other families simple aggregation occurs and pheromones play a part, but in some Sminthuridae (Bourletiellini and Sminthurini) there may be an elaborate dance, in which the male grasps the female by means of the specialised spines and hairs on the antennae, head or legs and directs her to the spermatophore. Some soil-dwelling Collembola are parthenogenetic. In all adult Collembola examined a reproductive instar alternates with a shorter, non-reproductive feeding instar, each period of the cycle being separated by an ecdysis. In the females of some species the external morphology of the reproductive instar differs markedly from that of the non-reproductive instar. This phenomenon is called epitoky. Periods of stress (such as intervals of food deprivation caused by drought or adverse temperatures), can induce quiescence or dormancy; this can result in synchronisation of life history within a population since a feeding phase and then moult follows amelioration of the adverse conditions. Eggs are laid singly or in clusters in the soil or leaf litter and in *Sminthurus viridis*, *Arrhopalites* and some other Symphypleona are covered with freshly eaten soil mixed with a rectal fluid voided through the anus after oviposition. This covering protects the eggs against dehydration and fungal attack. In other species (e.g. *Folsomia candida*) eggs are kept free of fungal hyphae by grazing of the adults.

The life histories of few Collembola have been studied in detail in Australia. The introduced, clover springtail *S. viridis*, has received greatest attention since it is regarded as a pest of pastures in winter rainfall areas of southern Australia. The aestivating eggs hatch with autumn rains and the juveniles pass through 5 (male) or 6 or more (female) instars before maturity, usually becoming adult 3-5 weeks after hatching, depending on temperature. The female lays several batches of eggs during her lifetime. There are 3-4 generations from autumn to late spring, when high temperatures and low rainfall bring about the disappearance of the active stages. Eggs in diapause are laid in the spring, and diapause development is completed in the field by mid-summer, after which the eggs hatch when rainfall and temperature again become favourable (Wallace 1967, 1968). Summer active taxa such as *Corynephoria* species probably have winter diapausing eggs.

Ecology. Collembola are found predominantly in the soil and in leaf litter and other decomposition habitats such as logs and dung. Certain species are found on grasses, in flowers and under the bark of trees. Collembola are virtually ubiquitous, being found in all terrestrial biomes, including mountain tops, polar regions and deserts. Many species inhabit caves. They are common also in marine and fresh water littoral habitats, occur interstitially in wet sand, on and under rocks including coral reefs, and on

water surfaces. However, very few truly aquatic species have yet been recorded. Collembola are often encountered in animal nests including those of vertebrates and social insects. Some species seem to be distributed readily by agencies such as air currents or surface run off. Relative humidity is one of the most important factors determining activity and distribution, but Collembola can also be attracted to high carbon dioxide concentrations and other metabolites produced from micro-organisms. Other factors influencing distribution are the location of food, temperature and soil pore space.

Most species feed on micro-organisms associated either with the rhizosphere, with decomposing organic matter or to a lesser extent with the aerial surface of plants; they do not feed readily on sterile, decayed leaves. Some Collembola feed on the faecal pellets of other soil invertebrates. Although many species are considered relatively unselective in their feeding habits, preference feeding experiments and morphological variation in mouth-parts indicate that selection of micro-organisms can take place and that the nutritional value of the food influences feeding behaviour. A few species feed on pollen and a small number are predacious. *Friesea* species feed on tardigrades and rotifers, and some Brachystomellidae on bacteria, nematodes and Protozoa. The only species in Australia known to feed preferentially on live plant material is *S. viridis* although some others (*Onychiurus* spp) at times feed on roots. Juveniles of *S. viridis* may feed actively upon recently dead adults, and in so doing ingest accumulated urates that hasten their own death. This process plays an important part in regulating the population density of this pest (Wallace 1967). Some species are said to feed on decaying animal matter (e.g. *Yuukianura* on dead earthworms) and others will eat their own exuviae. The Neanurinae digest externally and ingest the liquid products. The alimentary canal is well supplied with glycosidases but cellulases are in low concentration. Through their interactions with micro-organisms, Collembola are thought to act as catalysts in the breakdown of organic matter and in the cycling of plant nutrients and through their feeding and other activities and the deposition of faecal material they can alter the physical properties and structure of soils.

The collembolan fauna of Australia's arid and semi-arid areas is unexpectedly diverse given the group's general dependence on high humidities. Survival of adverse dry periods involves a range of adaptations including apparent anhydrobiosis (Greenslade 1982a) and water resorption from the faeces. After rain, populations of anhydrobiotic species rehydrate and are active until conditions become dry again. Densities in arid regions are highly variable although on average they are low (2000–3000/m²), about an order of magnitude lower than those of sown pastures in Australia (20 000–30 000/m²) (King and Hutchinson 1976). These pastures tend to carry a higher proportion of non-native species than do pastures of native grasses (King *et al.* 1985). Collembola can also be very abundant (*ca.* 100 000 animals/m²) on subantarctic islands such as Macquarie I. although species richness is low. In areas experiencing a mediterranean climate,

ecomorphic species occur which ecdyse to a desiccation resistant summer morph. In isotomid and hypogastrurid Collembola for instance, this resting stage remains in the soil until breaking rains of autumn. Cyclomorphosis is a similar phenomenon but here both morphs remain active.

Collembola generally are sensitive indicators of disturbance and therefore of value in environmental assessment. Quantitative methods using Collembola to measure the degree of disturbance of a habitat are being developed (Greenslade and Greenslade 1987).

Many aspects of the physiology of Collembola have been studied. Among these are osmoregulation, salt tolerance, cold hardiness, regulation of water loss and heavy metal contamination (Joosse and Verhoef 1987) and it is known for instance that some species can regulate water and salt loss over a wide range of conditions. The application of low levels of insecticides may contribute to a rapid increase in collembolan numbers, since many Collembola tolerate these chemicals while their predators are killed. Some Collembola can tolerate heavy metal contamination of the environment by concentrating these elements in the epithelial cells of the intestine which are eliminated at ecdysis and others are resistant to damage from radiation. Work done recently on cold adaptation of Antarctic and montane Collembola shows that some species are remarkably cold-tolerant; high concentrations of glycols and sugars in body fluids seem to protect these cold-adapted forms from freezing. In temperate Collembola a different mechanism involving thermal historesis proteins in the haemolymph appears to be operating.

In conclusion, the Collembola can be considered an extremely successful group using the criteria of E. O. Wilson (1987): they occupy a major adaptive zone, (i.e. feeding on micro-organisms), are ubiquitous or nearly so and given their presence in the Devonian, they exhibit extraordinary persistence in time.

Natural Enemies. Many predacious arthropods prey on Collembola as do coral reef fish, wading birds, small marsupials, reptiles and frogs. The predatory arthropods, some of which have evolved elaborate catching devices, include carabid and staphylinid beetles, dacetine ants, Hemiptera, empidid and dolichopodid flies, spiders, Opiliones, pseudoscorpions, centipedes and prostigmatid and mesostigmatid mites. Collembola seem to be the main diet of bdellid, cunaxid and anystid mites and in Australia, *Bdellodes lapidaria* feeds on *S. viridis*, and plays a role in its biological control. Viruses, bacteria, fungi and Protozoa as well as nematodes have been found to be parasites of Collembola. Apart from leaping and cryptic coloration, Collembola have a number of defence mechanisms against predation. These include immobility, mimicry and a spiny dorsum; onychiurids and hypogastrurids produce distasteful secretions.

Economic Significance. The only serious collembolan pest is *S. viridis* which feeds on clover in improved pastures in southern Australia. *Hypogastrura* species are pests of mushroom cultures and beds are routinely fumigated as a control measure. Species of *Onychiurus* and *Folsomia candida*, which can feed on roots of seedlings and bulbs respectively, occasionally cause economic dam-

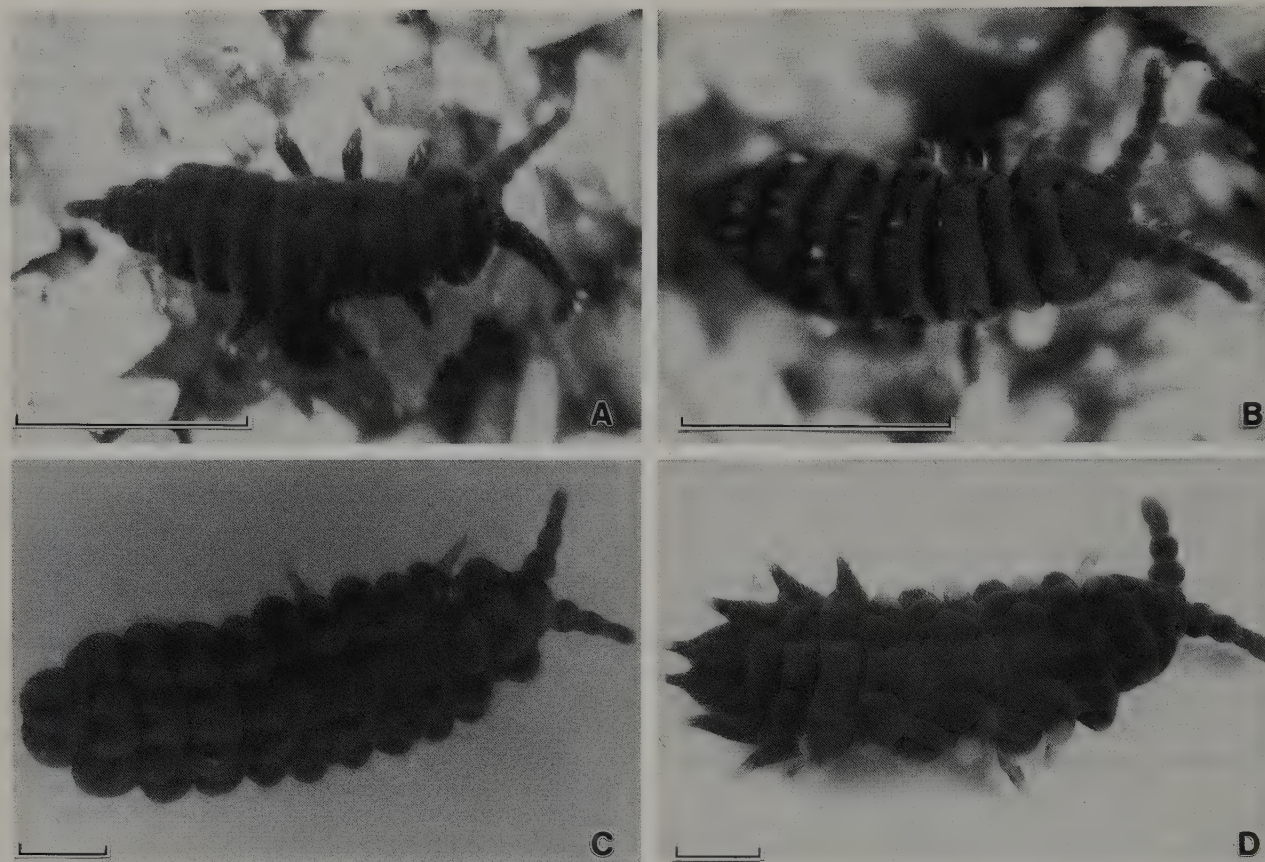


Fig. 11.4 Neanuridae: A, *Pseudanurida glauerti*, Pseudachorutinae, ♂; B, *P. glauerti*, ♀; C, *Megalanura tasmaniae*, Uchidanurinae; D, *Womersleymeria* sp., Uchidanurinae. Scales = 1 mm. [A–C photographed by J. Forrest; D by J. Green]

age in horticultural situations. The subject has been reviewed for Australia by Greenslade and Ireson (1986) where a key is given to species of agricultural importance. Collembola generally are beneficial to soils in enhancing fertility.

Special Features of the Australian Fauna

The Australian fauna has four main elements: a cosmopolitan element which can be divided between recent and ancient groups; a group with southern affinities; an

Australian autochthonous group; and a group with northern affinities. The proportion that each of these components contributes to any local or regional fauna depends on climate, latitude and vegetation. The zoogeography of arid zone and of Tasmanian Collembola have been discussed at the generic level by Greenslade (1982a, 1987). About half the genera occurring in Australia are cosmopolitan while a quarter are endemic. Only about 20% of the fauna is named and there are many undescribed, endemic species.

CLASSIFICATION

Class COLLEMBOLA (1630 Australian spp.)

Order ARTHROPLEONA (1160)

PODUROIDEA (405)

1. Neanuridae (220)
2. Odontellidae (60)
3. Brachystomellidae (70)
4. Hypogastruridae (35)
5. Onychiuridae (20)
- Poduridae (0)

ENTOMOBRYOIDEA (755)

6. Isotomidae (300)
7. Entomobryidae (300)
8. Paronellidae (70)
9. Cyphoderidae (30)
10. Oncopoduridae (5)
11. Tomoceridae (50)

Order NEELIPLEONA (20)

12. Neelidae (20)

Order SYMPHYPLEONA (450)

14. Dicyrtomidae (50)

13. Sminthuridae (400)

- Actaletidae (0)
- Coenaletidae (0)
- Microfalcidae (0)
- Protentomobryidae (0)

- Mackenziellidae (0)

The classification adopted here is revised from that of Wallace and Mackerras (1970) by additions from Massoud (1971b, 1976), W. R. Richards (1968), Szeptycki (1979), Betsch (1980) and Fjellberg (1985b). Families have increased from five to 14 since the 1st edition, caused by splitting existing families and not by new family records for Australia.

There have been a number of attempts to determine relationships between the families of Collembola, and at present the two most primitive families are thought to be

the Hypogastruridae and Isotomidae while the Entomobryidae, Sminthuridae and Neanuridae are believed to be more advanced (Massoud 1967). However, a convincing phylogenetic tree has not yet been established. A Devonian fossil known from the Rhynie Chert of Aberdeenshire, *Rhyniella praecursor*, has features in common with the Isotomidae, but the deposit contains more than one species (Greenslade 1988). There has been a suggestion that the specimens are Tertiary contaminants, but there is no evidence to support this contention.

Key to the Families of Collembola Known in Australia

1. Body globular (Figs 11.1B, 8), thoracic segments 2 and 3 and anterior abdominal segments 1–4 fused; mouth opening ventral to ocelli (hypognathous) 2
- Body elongate (Figs 11.1A, 5–7), the majority of segments well separated; mouth opening anterior to ocelli when present (prognathous) 4
- 2(1). Antennae shorter than head length (Fig. 11.8D); ocelli absent; bothriotricha absent, sensory areas present on greater abdomen; body and head together less than 0.5 mm long; adult white, yellow or grey **Neelidae**
- Antennae longer than head length; ocelli nearly always present; bothriotricha present, sensory areas absent on greater abdomen; adults usually darkly pigmented and more than 0.5 mm long 3
- 3(2). Distal antennal segment shorter than the penultimate antennal segment (Fig. 11.8C) **Dicyrtomidae**
- Distal antennal segment equal to or longer than the penultimate antennal segment (Figs 11.1B, C, 8A, B, E) **Sminthuridae**
- 4(1). Thorax 1 developed, tergum with setae; body segments about equal in length (Fig. 11.5) 5
- Thorax 1 not developed, tergum without setae; body segments not always equal in length (Figs 11.1A, 6, 7) 9
- 5(4). Mandible with granular, ridged molar plate (Fig. 11.2A) 6
- Mandible, if present, without ridged molar plate (Figs 11.2B, G) 7
- 6(5). Pseudocelli present (Fig. 11.3E); furca absent; antenna 3 organ complex, with 2–3 large, rod-shaped sensilla and 3 sensorial bodies behind 4–5 finger-like papillae (Fig. 11.3D); postantennal organ elongate with more than 6 vesicles (Fig. 11.3B); blind, white or yellowish species (Fig. 11.5F) **Onychiuridae**
- Pseudocelli absent; furca nearly always present; antenna 3 organ simple, with only 2–3 rod-shaped sensilla, no papillae or sensorial bodies; postantennal organ, if present, usually round or oval with a maximum of 6 vesicles (Fig. 11.3F); body usually pigmented and ocelli usually present (Fig. 11.5E) **Hypogastruridae**
- 7(5). Mandible absent; maxilla with toothed head (Figs 11.2D, E); buccal cone flattened and blunt **Brachystomellidae**
- Mandible present, sometimes difficult to see and positioned close to anterior border of clypeus; maxilla either pointed or with narrow toothed head (Figs 11.2C, F); buccal cone cone-shaped and pointed 8
- 8(7). Mandible sometimes apparently absent, and aligned along anterior border of clypeus; thorax 3 without microsensilla; cardo absent; antennae conical; buccal cone broadly conical; furca present (Fig. 11.5B) **Odontellidae**
- Mandible always present, not aligned along anterior border of clypeus; thorax 3 with microsensilla; cardo present between stipes and fulcrum; antennae nearly cylindrical; buccal cone pointed; furca sometimes absent (Fig. 11.5A) **Neanuridae**
- 9(4). Abdominal segment 4 distinctly longer than 3 (Figs 11.7A, B, D, F); postantennal organ absent; chaetotaxy consisting of short and long, serrated setae; scales sometimes present 10
- Abdominal segment 4 not longer than 3 (Figs 11.6, 7C, E, G); postantennal organ usually present; chaetotaxy variable but usually consisting of short, simple setae; long setae, if present, not densely ciliated 12
- 10(9). Dens curved, slender, tapering and annulated; mucro hook-like, with 1 or 2 teeth and usually a short spine **Entomobryidae** (pt)
- Dens straight, stout, neither tapering nor annulated; mucro not hook-like, usually with more than 2 teeth 11
- 11(10). Dens with fringed, scale-like setae (Fig. 11.7F); mucro narrow, at least 3 times longer than pretarsal claw; blind, white **Cyphoderidae**
- Dens without fringed, scale-like setae (Fig. 11.7B); mucro broad, shorter than or equal in length to pretarsal claw; ocelli and dark pigment usually present **Paronellidae**
- 12(9). Antenna 1 subdivided into 2 segments (Fig. 11.7E) **Entomobryidae-ORCHESELLINAE**
- Antenna 1 not subdivided 13
- 13(12). Scales usually present on body (Figs 11.7C, G); abdomen 3 usually slightly longer than 4; antenna 3 longer or equal to 4; mucro often with several setae or spines and usually 4 or more teeth 14
- Scales absent (Fig. 11.6); abdomen 3 shorter or equal to 4; antenna 3 shorter than 4; mucro never with spines and with a maximum of 4 teeth **Isotomidae**
- 14(13). Blind (Fig. 11.7C); white or light grey; postantennal organ present with rosette of elongate tubercles **Oncopoduridae**
- Ocelli present, 6+6 or 8+8 on each side (Fig. 11.7G); body with some dark pigment; postantennal organ usually absent in adults, if present simple with single vesicle **Tomoceridae**

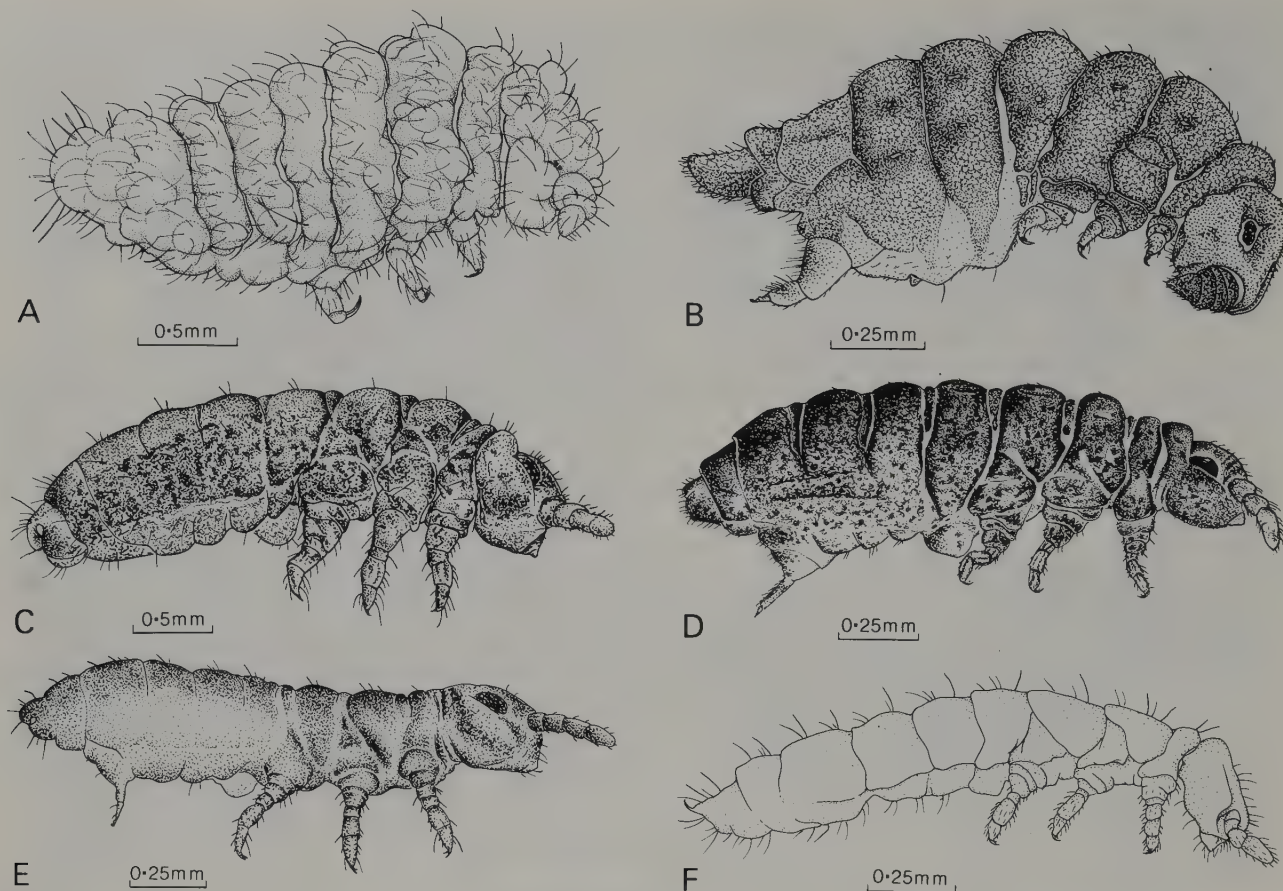


Fig. 11.5 A, Neanuridae-Neanurinae; B, *Odontella* sp., Odontellidae; C, *Setanodosa* sp., Brachystomellidae; D, *Austrolella* sp., Brachystomellidae; E, *Xenylla* sp., Hypogastruridae; F, *Tullbergia* sp., Onychiuridae.
[J. Thurmer]

Order ARTHROPLEONA Superfamily PODUROIDEA

1. Neanuridae. Four subfamilies differing in their mouth-parts are recognised and all occur in Australia. These subfamilies are found predominantly in the more humid parts of Australia and there are few species in the arid zone. The FRIESEINAE are a small subfamily consisting of a single, cosmopolitan genus, *Friesea*, which has a number of undescribed species in Australia and 2 described species on Macquarie I. The NEANURINAE, which live in logs and sticks and are usually white, pink, orange or red, are dorsoventrally flattened and lack a furca (Fig. 11.5A). Several genera are represented in Australia, including *Australonura* (14 spp.) (Greenslade and Deharveng 1990) which extends into the South-West Pacific and has 2 species on Norfolk I. Polytene chromosomes are found in the salivary glands of those neanurines which digest food externally. The PSEUDACHORUTINAE are taxonomically the least known subfamily and the Australian fauna contains undescribed genera and numerous undescribed species. *Pseudachorudina* (2 spp.) is known from a large species from the Snowy Mountains and another species from Tas. One marine, littoral genus, *Oudemansia* (2 spp.) is associated with coral reefs, and

Pseudanurida (2 spp.) (Figs 11.4A, B) also occurs around Australian shores.

UCHIDANURINAE are an ancient subfamily, whose species are associated with decaying logs and moss in temperate and subtropical rainforests. Three genera are known: *Womersleymeria* (1 sp.) (Fig. 11.4D) and *Acanthanura* (1 sp.) which are endemic to Australia, and *Megalanura* (1 sp.) (Fig. 11.4C), endemic to Tas. There are several, additional, undescribed species; all are large, spectacular and of considerable biogeographic and phylogenetic importance.

2. Odontellidae. This family has many Australian species yet to be described in the cosmopolitan genus *Odontella* (Fig. 11.5B). Odontellids are extremely common in leaf litter in the humid forests of south-eastern Australia and Tas., but *Caufrenyllodes*, the only endemic genus, occurs predominantly in sub-humid and seasonally arid areas. A key to the genera of Odontellidae in Australia is given in Greenslade and Deharveng (1984).

3. Brachystomellidae (Figs 11.5C, D). This family, in which the mandibles are completely absent, is very well developed in southern, humid parts of the continent, where species are often associated with fungal fruiting bodies and probably feed on fungal spores (e.g. *Sub-*

clavontella, 2 spp.). Members of other genera are found in leaf litter and on grasses in damp situations. *Brachystomella parvula* has been recorded by Womersley (1939) as common in Australia, particularly in pastures but this has not been confirmed. The record was probably a misidentification for *Brachystomella platensis*, a species widely distributed in the Southern Hemisphere and recorded by Greenslade and Najt (1987b). *Setanodosa* (3 spp.) is predominantly arid or semi-arid in distribution and has been observed swarming in enormous numbers under mallee vegetation. *Rapoportella* is known only from a species on Kangaroo I. and several species from the Americas.

4. Hypogastruridae. In Australia this is a small and relatively well known family of 7 genera generally found in leaf litter and in the upper levels of the soil; a few species occur in caves while some live under bark. Since *Hypogastrura* (8 spp.) is predominantly Holarctic and all Australian species are also known from Europe, it is probable that all species in Australia are introduced. They are mainly found in cool, humid climates, and in habitats that have been disturbed by man. *H. (Ceratophysella) denticulata* is one of the commonest species in urban situations and on agricultural land (King *et al.* 1985). *H. (Hypogastrura) viatica*, which swarms beside brackish marshes and lagoons, has a distribution extending to Macquarie I. and is common in the Arctic also. In contrast to *Hypogastrura*, *Triacanthella* and *Xenylla* (16 spp.; Gama 1974, 1980; Gama Assalino and Greenslade 1981) are native and most species are endemic to Australia. *Xenylla* (Fig. 11.5A) tolerates drier habitats than *Hypogastrura*, and is less common in the very cool areas in the south. *Paraxenylla* (1 sp.) and *Xenylla* both include littoral species. There are a number of undescribed species of *Triacanthella*, a genus with a boreal and austral distribution.

5. Onychiuridae. This small, soil-living family is characterised by the presence of pseudocelli (Fig. 11.3E) which secrete fluid. Two of the three subfamilies occur in Australia. ONYCHIURINAE are most diverse in the Northern

Hemisphere and probably all Australian species, some of which are pests, are introduced. The subfamily TULLBERGINAE has both Southern and Northern Hemisphere elements and is one of the commonest collembolan subfamilies on subantarctic islands, where it is represented by *Tullbergia* (Fig. 11.5F).

Superfamily ENTOMOBRYOIDEA

6. Isotomidae. Many isotomid genera, particularly those that live in the soil, are cosmopolitan. Their gross morphology (Fig. 11.6) can be related to the position in the soil profile in which they live. A few genera are marine littoral. *Axelsonia* is found in crevices in rocks, *Archisotoma*, interstitially in sand around Australia and *Psammisotoma* on beaches of the Great Barrier Reef (Greenslade and Deharveng 1986). In some regions with severe climates, such as the Subantarctic, species of *Cryptopygus* can be extremely abundant and numerically dominate the collembolan faunas. In contrast, *Folsomides* (40 spp.) is highly diverse and abundant in arid areas. *Folsomotoma* is known from the sub-antarctic islands, New Zealand and the cooler parts of Australia; *F. bioculata* occurs in rainforest leaf litter in Vic. (Greenslade 1986a). *Isotomurus palustris*, a cosmopolitan species, is one of the most abundant collembolans in improved pastures.

7. Entomobryidae. This is a large family of elongate species. All subfamilies occur in Australia. The ENTOMOBRYINAE, SEIRINAE and LEPIDOCYRTINAE have abdomen 4 much longer than 3 and an undivided antenna 1, while the ORCHESSELLINAE have abdomen 3 approximately equal to abdomen 4 and antenna 1 and sometimes antenna 2 subdivided. There are only 3 genera of Orchesellinae in Australia: *Australotomurus* (6 spp.) (Fig. 11.7E) is epigaeic and endemic to southern Australia (Mari Mutt and Greenslade 1985); *Heteromurus* and *Dicranocentrus* live in leaf litter in tropical areas. The remaining subfamilies are larger and have species in a wide range of habitats including leaf litter, soil, under bark and on vegetation. Species of *Entomobrya*, some of which are probably

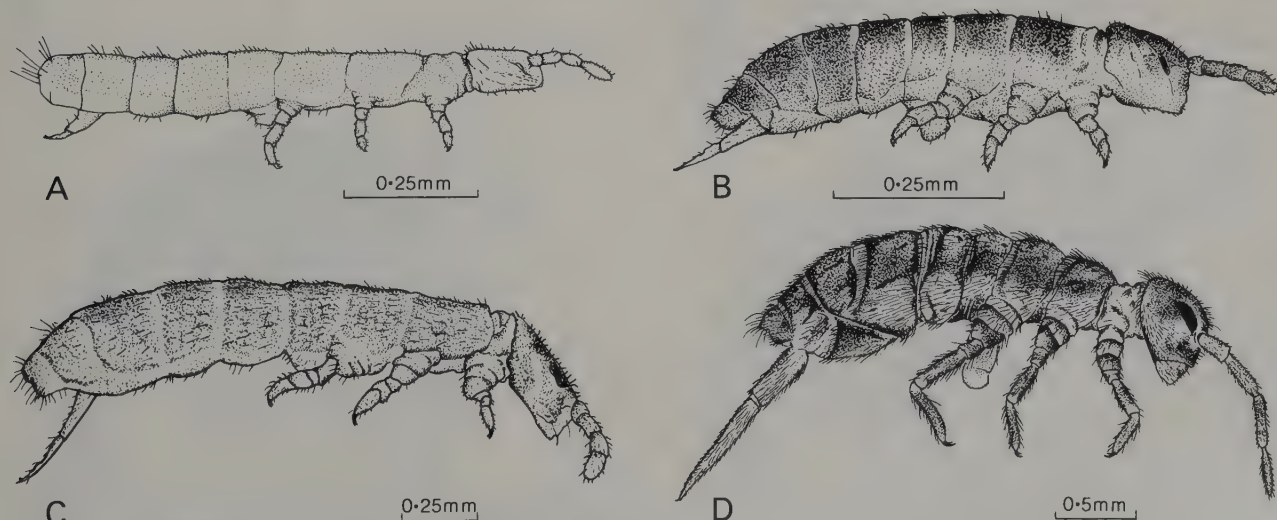


Fig. 11.6 Isotomidae: A, *Isotomodes* sp.; B, *Proisotoma brisbanensis*; C, *Folsomides* sp.; D, *Acanthomurus* sp.

[J. Thurmer]

introduced from Europe, are common in sown pastures. *Lepidocyrtus* is a large, cosmopolitan genus with many undescribed species which are abundant in forest leaf litter in Australia. *Isotobrya* (2 spp.) is a rare, endemic genus from termite nests. *Lepidosinella* (1 sp.), also known from Java, has been recorded from caves in N.S.W., and *Drepanura* (5 spp.; Fig. 11.7D) is common in arid regions.

8. Paronellidae. In Australia this is a small family and only 5 genera are known. Apart from a littoral species and an undescribed cavernicole all members of the family are epigaeic and live on trees, shrubs, epiphytes or grasses or in leaf litter. Species are almost entirely restricted to humid tropical and southern cool temperate zones where they are often abundant. They are not found in arid or semi-arid areas. *Metacoelura* (2 spp.), the only endemic

genus, occurs on grasses in northern tropics, and *Pseudoparonella* (2 spp.; Fig. 11.7B) in tropical and temperate rainforest leaf litter. *Salina* (1 sp.), a pantropical genus, occurs in lowland, tropical rainforest in northern Qld, and *Paronellides* (2 sp.) is a southern genus also found in New Zealand with many undescribed species in Tas. *Paronellides mjobergi*, described from Qld, is very abundant in N.S.W. and Vic., occurring from the coast to high altitudes in the Snowy Mtns.

9. Cyphoderidae. All species of this family are inquilines in the nests of ants or termites. There has been no recent work on the Australian fauna and there are undescribed species and possibly genera in Australia. *Cyphoda nicholli* is frequently encountered in nests of the ant *Rhytidoponera metallica*.

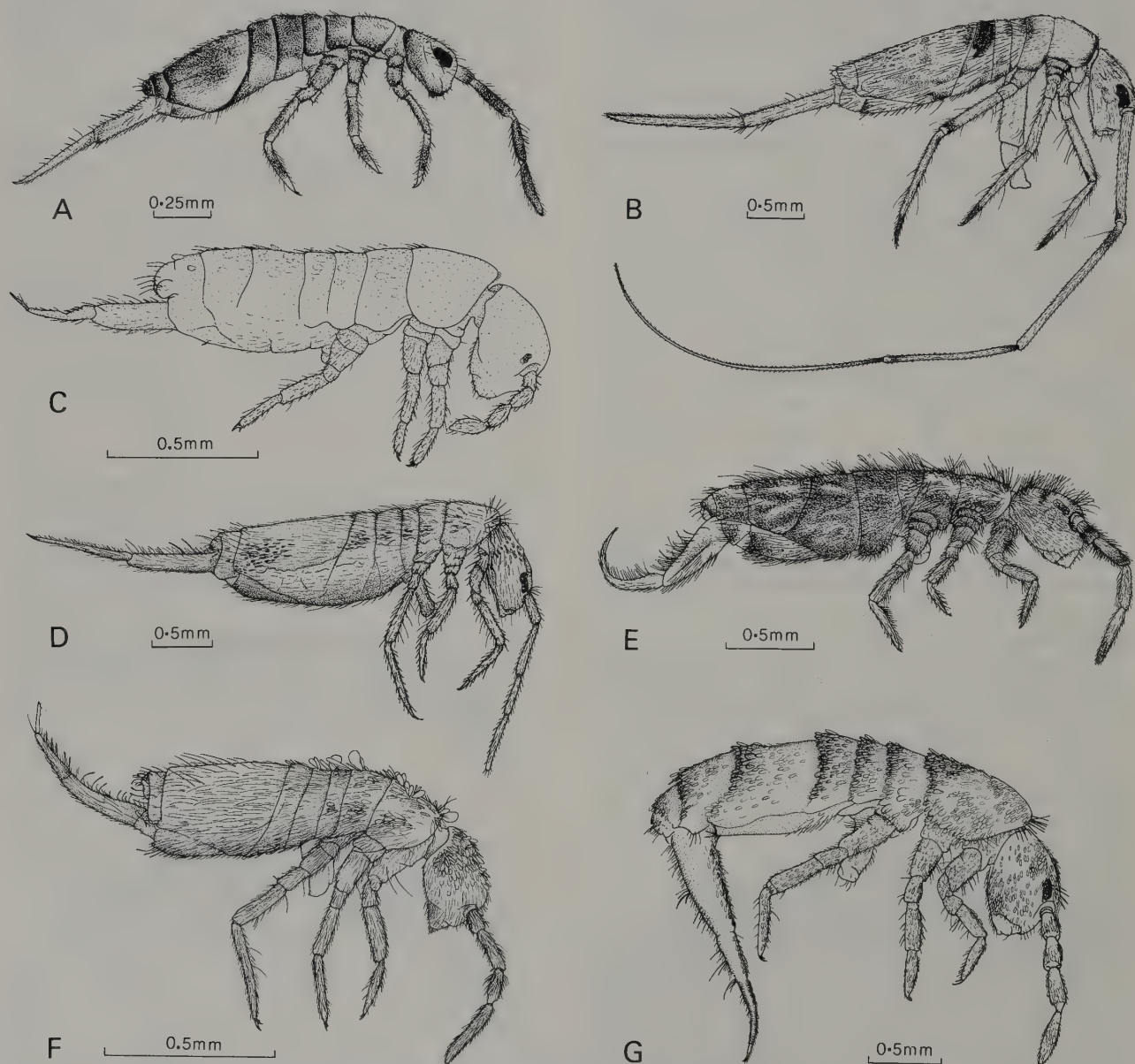


Fig. 11.7 A, *Drepanura* sp., Entomobryidae; B, *Pseudoparonella queenslandica*, Paronellidae; C, *Oncopodura tiegsi*, Oncopoduridae; D, *Acanthurella* sp., Entomobryidae; E, *Australotomurus johanni*, Entomobryidae; F, Cyphoderidae; G, *Lepidophorella* sp., Tomoceridae. [J. Thurmer]

10. Oncopoduridae. This is a rare family of cave- and soil-living forms. In Australia *Oncopodura* (1 sp.; Fig. 11.7C) is known from leaf litter and rotting logs in *Nothofagus* rainforests in southern Vic. and Tas. An undescribed species is known from caves.

11. Tomoceridae. This family of large and conspicuous Collembola is mainly Holarctic and uncommon in Australia, although *Lepidophorella* (Fig. 11.7G) has a typically southern distribution and is found in leaf litter of cool, moist forests. *Novacerus* is uncommon and known from a species in Tas. and 2 in New Zealand. At least one undescribed genus is known from Tas.

Order NEELIPLEONA

12. Neelidae (Fig. 11.8D). This is a cosmopolitan family of minute, globular, soil-living forms. There are only 3 genera which are very poorly known both in Australia and world-wide. They can be abundant in moist, tropical soils. A *Megalothorax* species has been collected on Macquarie I.

Order SYMPHYPLEONA

13. Sminthuridae. Sminthurids are also globular springtails and 3 subfamilies are generally recognised; all occur in Australia. Practically all species of all subfamilies are epigeic and either live in and on the upper layers of leaf litter, on grasses or on other low vegetation. The SMINTHURIDINAE are fairly small Collembola which exhibit marked sexual dimorphism; the antennae of males are furnished with hooks and spines (Fig. 11.1C). *Sminthurides* is aquatic. Minute *Sphaeridia* spp. (Fig. 11.8B) of arid and semi-arid areas, have a short life history of about a week; this can be completed during brief periods of high humidity after rain. The KATIANNINAE is a subfamily of predominant southern distribution, well developed in cool humid parts of Australia, and containing some undescribed genera. *Adelphoderia* (1 sp.) belongs to the Spinothecini (sometimes treated as a separate subfamily); the pair of sacs which encircle the neck in members of this remarkable tribe probably act as accessory respiratory organs. *A. regina* occurs in

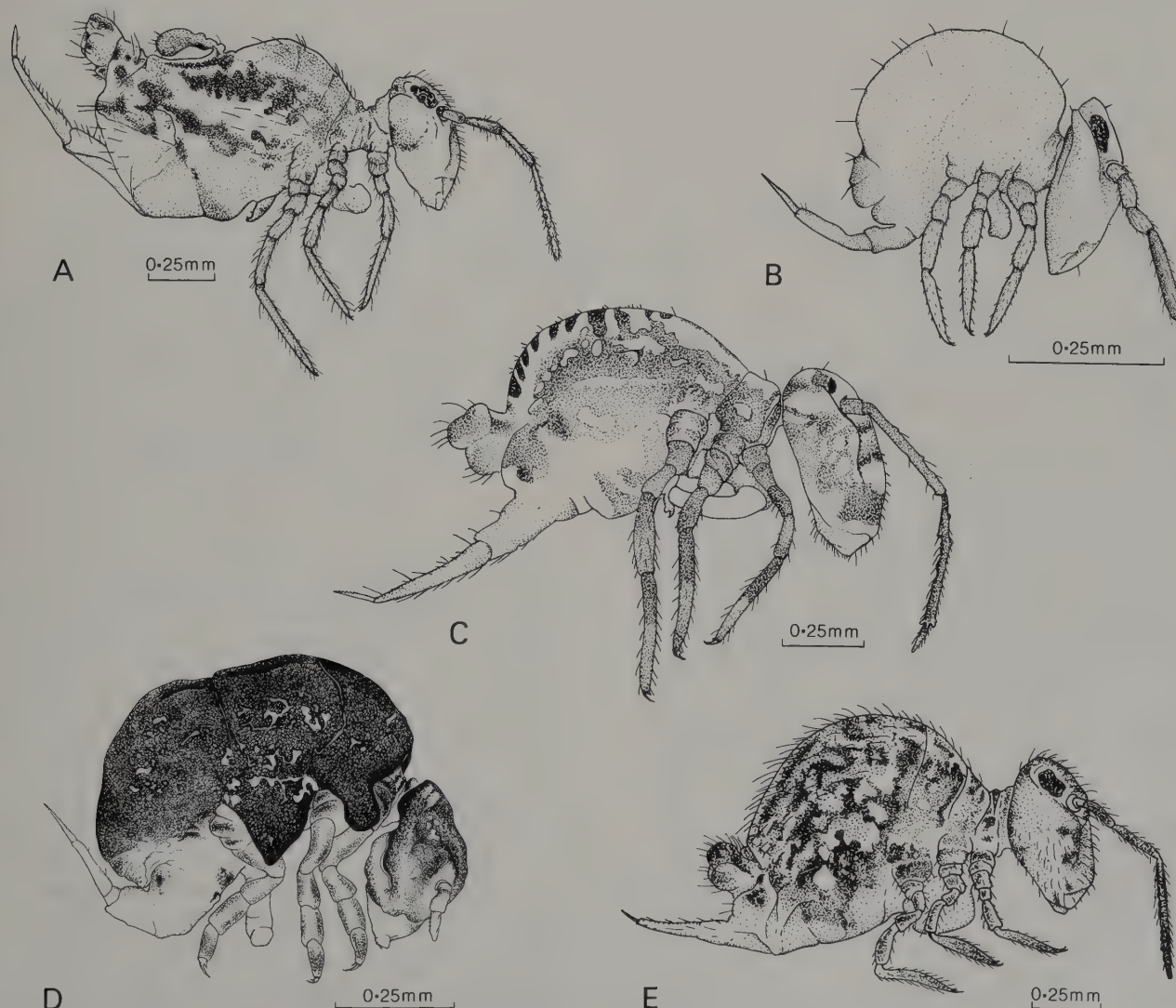


Fig. 11.8 A, *Corynephoria* sp., Sminthuridae; B, *Sphaeridia* sp., Sminthuridae; C, *Dicyrtoma* sp., Dicyrtomidae; D, *Neelides* sp., Neelidae; E, *Katianna* sp., Sminthuridae.

[J. Thurmer]

Australian *Nothofagus* forests (Greenslade 1982b) and undescribed species are known from caves; otherwise the tribe is known only from New Zealand and South America. *Katianna* (Fig. 11.8A) is a diverse genus living in grass and leaf litter in southern parts of Australia and northern upland areas; some native species colonise sown pastures. The subfamily SMINTHURINAE contains two tribes, the Sminthurini and the Bourletiellini. Sminthurini have taxa centred on the Northern Hemisphere and tropics and some, *Sminthurus viridis*, for example, have been recently introduced to Australia. *Temeritas* (3 spp.), a native genus with very long antennae, is found under logs in humid forests, and also occurs in South-East Asia and on South Pacific islands. *Neosminthurus* is known from montane, tropical forests in Qld. The Bourletiellini are very well developed in Australia and species possess tracheae which help them tolerate hot dry conditions. *Corynephoria* (Fig. 11.8C; Greenslade 1977) and *Rastriopes* both have undescribed species in arid and

semi-arid areas. *Corynephoria* may carry a heavy load of ectoparasitic mites in arid regions (Greenslade and Southcott 1980). Some Bourletiellini are sexually dimorphic: e.g. males of *Nasosminthurus* have a complex, spinose facial organ (Wallace 1974) and males of *Bourletides* have antennal hooks.

In parts of Australia with a mediterranean climate, there are seasonal differences in the activity of the epigaeic sminthurids. *Corynephoria* hatch as the soil warms in late spring and are active through the summer until autumn. Autumn rain stimulates hatching of Katianninae which are active throughout autumn and winter until eliminated by the high temperatures and desiccating conditions in late spring.

14. Dicyrtomidae (Fig. 11.8E). This family is treated as a subfamily of the Sminthuridae by W. R. Richards (1968). Species are epigaeic and are found in the ground layer of forests and woodlands. The family has been little studied in Australia.

Protura

G. IMADATÉ

Very small, entognathous hexapods, mostly unpigmented; antennae absent; legs 5-segmented, fore leg modified for sensory purposes; abdomen 12-segmented in adult, with appendages on segments 1–3; cerci absent. Ovaries meroistic; spermatozoa non-motile. Juvenile development anamorphic.

Protura are pale, delicate, cryptic arthropods, which are less than 2 mm long and move slowly (Fig. 12.1A). They were first recognised by Silvestri (1907). They are rarely seen except in samples from 'Berlese' funnels, but are known from all zoogeographical regions and about 500 species have been described world-wide. Tuxen (1967) has reviewed the Australian species.

Anatomy of Adult

Head. Prognathous, almost completely enclosed ventrally, with the basal part of labium eliminated, and only the tips of the mouth-parts showing anteriorly. Antennae and eyes absent. A pair of pseudoculi with olfactory or chemosensory functions. Mouth-parts (Fig. 12.2) slender; mandibles styliform; maxillae with elongated galea and lacinia, maxillary palp 3-segmented, ending in a tuft of setae; labium apically bilobed, each part triangular, labial palp usually 1-segmented, ending in a tuft of setae similar to the maxillary palp or reduced, with a few setae and a sensillum. Canal of maxillary gland (filamento di sostegno) opening into the atrial cavity at the inner base of the lacinia of the maxilla (François and Dallai 1986).

Thorax. Segments clearly distinguishable. Prothorax reduced dorsally, but enlarged ventrally. In the Eosentomoidea spiracles present on the meso- and metaterga (Fig. 12.1c), their tracheae not meeting, but tracheoles run throughout the body. Legs 5-segmented. Mid and hind legs used for walking; fore legs longer than the others,

held forward in front of the head and used as antennae. Pretarsus ending in claw, ventral empodium and dorsal sensillum; sometimes with 2 or 3 small, tooth-like lobes (tunica lobes), these lobes sometimes connected by membrane (tunica).

Abdomen. Twelve-segmented in adult. Small 2- and 1-segmented abdominal appendages (styli) at the posterior corners of S1–3 (Fig. 12.3). Cerci absent; anus terminal. Abdominal gland a large reservoir and opening at posterior margin of T8. The gland lid sometimes pectinated and called 'combs'. The external genitalia of Protura are referred to as the *squama genitalis*. A deep genital pouch opens between S11 and S12, and encloses the protrusible genital armature. In both sexes there are 2 basal arms (apodemes) and 2 styli. The gonopore is on the styli, and double in the male, but between the styli, and single, in the female (Fig. 12.4). The stylus is sometimes divided into a proximal *basistylus* and distal *acrostylus* (Tuxen 1970c).

Internal Anatomy. Gut simple; pyloric region characterised by muscular sphincter and wide chamber; Malpighian tubules represented by 6 papillae (Dallai 1976; Dallai *et al.* 1986). Nervous system generalised, with 7 discrete abdominal ganglia. Ovaries paired, sac-shaped and meroistic, the yolk developing through autosynthesis (Klag and Bilinski 1984). In the male, testes joined anteriorly about the middle of the thorax. Spermatozoa non-motile with peculiar shapes: a protrud-

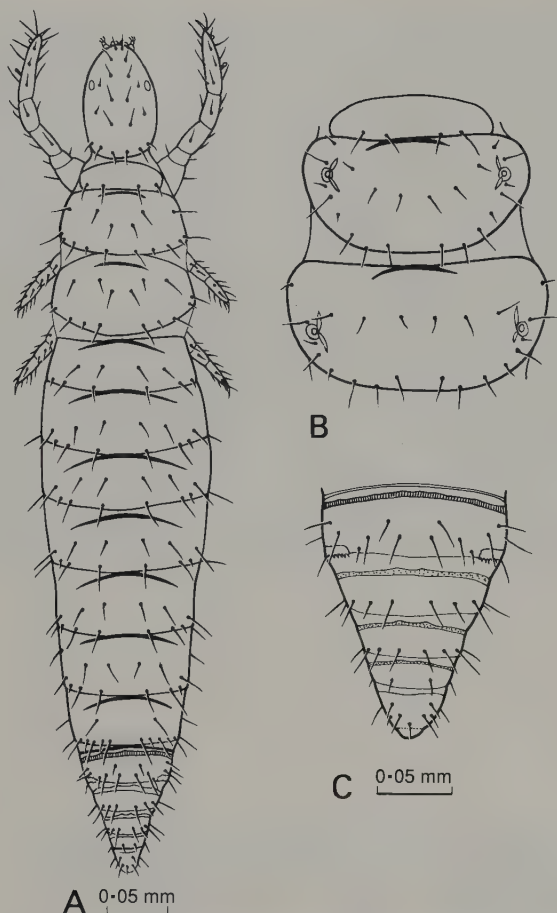


Fig. 12.1 Protura: A, *Australentulus tillyardi*, Acerentomidae, ♂, dorsal; B, thorax of *Eosentomon swani*, Eosentomidae, ♀, dorsal; C, *A. tillyardi*, distal abdominal segments enlarged. [A. Hastings]

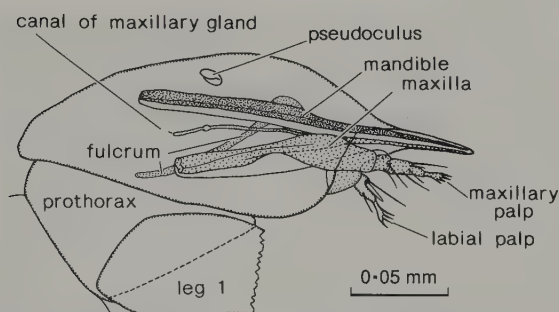


Fig. 12.2 Head of *Acerentomon* sp., Acerentomidae, in lateral section. [After Tuxen 1959]

ing straight or screw-shaped acrosome, helicoidally twisted nucleus and coiled, flagellated axoneme with 12+0, 13+0 or 14+0 doublets in acerentomids (Baccetti *et al.* 1973) and 9+9+2 or 13+0 in protentomids (Yin *et al.* 1985); or aflagellate and disc-shaped with no acrosome and no axoneme in eosentomids (Baccetti *et al.* 1973; Yin *et al.* 1987), aflagellate and globular in sinentomids (Dallai and Yin 1983).

Immature stages

The embryology is unknown. There is little change of form during growth, except for anamorphic increase in the number of abdominal segments (Bernard and Tuxen 1987). The larva ('prelarva', Fig. 12.5) has 9 abdominal segments on hatching, weakly developed mouth-parts and appendages, and develops into the larva I with 9 abdominal segments and fully developed mouth-parts and legs. The 3rd stage (larva II) has 10 abdominal segments. The 4th stage ('maturus junior') has 12 segments but incomplete chaetotaxy and no genital armature. Maturus junior moults to adult except in male Acerentomidae, which have an intervening pre-imaginal stage with incomplete genital armature. It is not known whether the adult continues to moult throughout its life.

Biology

Protura occur in soil, leaf litter, moss and occasionally in decaying wood. They are said to feed on mycorrhizal fungi. Life cycles of Australian forms have not been studied. In European acerentomids, the eggs apparently are laid in early spring and the adults overwinter, but in the eosentomids the young stages are found throughout the year. There may be more than one generation per year.

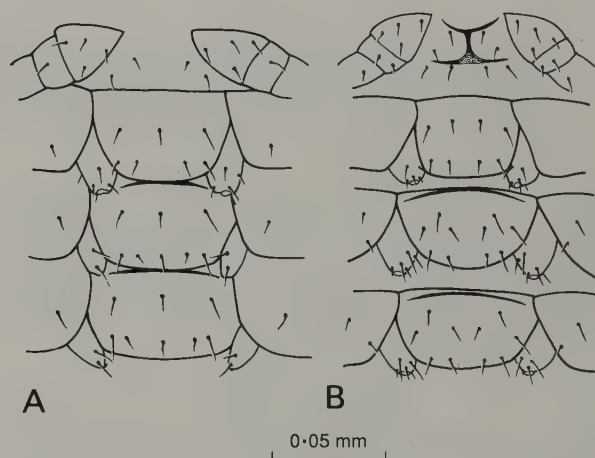


Fig. 12.3 Basal abdominal segments, ventral, showing rudimentary legs (abdominal appendages) of: A, *Australentulus tillyardi*, Acerentomidae; B, *Eosentomon swani*, Eosentomidae. [A. Hastings]

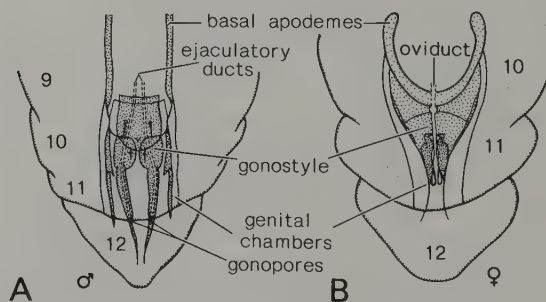


Fig. 12.4 Genital armature of *Eosentomon* sp., Eosentomidae. [After Tuxen 1970c]

CLASSIFICATION

Class and Order PROTURA
(30 Australian spp.)

Suborder EOSENTOMOIDEA (9)

1. Eosentomidae (9)
- Sinentomidae (0)

Suborder ACERENTOMOIDEA (21)

2. Protentomidae (1)
3. Acerentomidae (20)

A new 8-family classification was proposed by Yin (1983, 1984) on the basis of a revised proturan phylogeny. She considers that Acerentomoidea (which lack a tracheal system) comprise the primitive group, whereas Eosentomoidea (which do have a tracheal system) are a

more specialised group. This view contrasts with that of Tuxen (1963, 1964) or Imadaté (1966) but is supported by the recent, ultrastructural studies on proturan spermatozoa. Yin's family-categories are explained in the following section but her classification has not been followed.

Key to the Families of Protura

1. Tracheae and thoracic spiracles present or rarely reduced; abdominal segment 8 without striate band anteriorly EOSENTOMOIDEA. 2
- Tracheae and thoracic spiracles absent; abdominal segment 8 with striate band anteriorly (Figs 12.1A, B) ACERENTOMOIDEA. 3
- 2(1). Three pairs of 2-segmented abdominal appendages, with 5 setae on each appendage Eosentomidae
- 2nd and 3rd pairs of abdominal appendages 1-segmented, with 2 setae each Sinentomidae (China, Korea and Japan)
- 3(1). 1st pair, 1st and 2nd pairs (mostly), or all 3 pairs of abdominal appendages with terminal vesicles and at most 4 setae; striate band on abdominal segment 8 present as a single serrate line Protentomidae
- 2nd and 3rd pairs of abdominal appendages with no terminal vesicle and at most 3 setae; striate band on abdominal segment 8 present as a double line with or without striae Acerentomidae

Suborder EOSENTOMOIDEA

1. Eosentomidae. A large family of elongate forms; cosmopolitan. Mouth-parts fairly broad and sturdy. Mandibles blunt with small teeth apically; lacinia of maxilla hook-shaped; canal of maxillary gland without dilata-tions. Foretarsal empodium long; mid and hind claws knife-shaped without tunica. Abdominal segment 8 with-out pectinate ornamentations; lid over opening of abdomi-nal gland small, without teeth at hind border. Female with large, sclerotised areas (processus sternales), but no acrostyli. From Australia, one species of *Isoentomon* (*I. pseudosaharensis* from A.C.T.) and 8 species of *Eosentomon* are recorded. *E. swani* and *E. womersleyi* seem to be common in temperate rainforests and sclero-phyll woodlands in W.A., Vic. and A.C.T., and *E. wes-traliense* from dry sclerophyll woodlands in S.A. and A.C.T. *E. australicum*, known from temperate rainforests

in S.A. and Vic., is recorded from North America and *E. oceaniae*, collected from North Qld, is also found on the Solomon Is, Bismarck Archipelago (Tuxen and Imadaté 1975) and New Hebrides (Vanuatu), but the other six species are endemic to Australia.

The Chinese genus *Antelientomon* is exceptional among eosentomids in having the tracheae and thoracic spiracles reduced.

Suborder ACERENTOMOIDEA

2. Protentomidae. Body stout. Mouth-parts relatively sturdy. Lacinia of maxilla slightly hook-shaped or straight. Foretarsal empodium short. Mid and hind claws mostly boat-shaped with tunica lobes. Lid over opening of abdominal gland on abdomen 8 distinct, with or with-out teeth at the hind border. Female squama genitalis with bud-like or pointed acrostyli, but no processus sternales. Males rare.

Yin (1983) divided this family into 3 families as follows:

1. Metanotum with a pair of anterior setae and without middle setae; canal of maxillary gland without calyx; abdominal T1-7 with a central, anterior seta Fujientomidae (China and Japan)
- Metanotum with two pairs of anterior setae and one pair of middle setae; abdominal terga without central, anterior seta 2
- 2(1). Canal of maxillary gland with calyx sac-like, sausage-like or with oval dilatation proximally; pseudoculi open posteriorly Hesperentomidae (Asia, Europe and North America)



Fig. 12.5 Egg of *Eosentomon australicum*, Eosentomidae, containing prelarva.
[After Bernard 1976; A. Hastings]

The Chinese genus *Huhenomom* belongs to this group and is exceptional among protentomids in having the 2nd and 3rd abdominal appendages 1-segmented.

Canal of maxillary gland with calyx as bladder-like excrescence; pseudoculi never open posteriorly (*Protentomon*) Protentomidae
One female specimen of *Protentomon* is known from a dry woodland in A.C.T.

3. Acerentomidae. A large family of slender forms, occasionally with yellow tint. Mouth-parts always slender and prolonged; lacinia of maxilla long and pointed. Foretarsal empodium short or absent; mid and hind claws boat-shaped with a fully developed tunica. Lid of opening of abdominal gland on abdomen 8 with pectinate ornamentation. Female squama genitalis with pointed acrostyli, but no processus sternalis. Yin (1983) divided this family into 3 families as follows:

1. Labial palp ornamented with a few setae apically; canal of maxillary gland with simple calyx (5 genera in Australia) Berberentomidae
Labial palp ornamented with a tuft of setae apically 2
- 2(1). Canal of maxillary gland with simple calyx (2 genera, *Acerentulus* and *Australentulus*, in Australia) Acerentomidae
Canal of maxillary gland with racemous calyx
..... Acerellidae (Europe, Asia and North America)

Amphientulus (6 spp.) and *Tasmanentulus* (2 spp.) are known from Australia. These genera are mainly restricted to Australia and New Zealand (Tuxen 1986). *Amphientulus alienus* is known from wet sclerophyll forest in Vic., *A. ambiguus* from dry sclerophyll woodland in A.C.T. and *Tasmanentulus tasmanicus* from wet sclerophyll forest in Tas. and W.A. *Gracilentulus gracilis*, recorded from South Africa, Europe and New Zealand, is found in S.A. *Berberentulus capensis* is known from Africa, Europe, North America and N.S.W. *Baculentulus pseudonitidus* is known from W.A.

Acerentulus sexspinatus has been recorded from S.A. The genus *Australentulus* is known from Australia, New Zealand, tropical Asia (Imadaté 1989) and Madagascar. Among the 8 Australian species, *A. tillyardi* is most frequently recorded from many places in S.A., Vic., A.C.T. and N.S.W.

ACKNOWLEDGMENTS. Valuable comments on drafts of this chapter were provided by Professor C. Bernard, Department of Entomology and Plant Pathology, University of Tennessee, Knoxville, U.S.A.; Ms P. Greenslade, Canberra, Australia; Professor D. K. McE. Kevan, Department of Entomology, McGill University, Ste Anne de Bellevue, Canada, and Dr A. Szeptycki, Polish Academy of Sciences, Kraków, Poland.

COLOUR PLATES

PLATE 1

ODONATA

(Males)

- A *Synthemis eustalacta*, Corduliidae
- B *Nannophya occidentalis*, Libellulidae
- C *Austrogomphus guerini*, Gomphidae
- D *Cordulephya pygmaea*, Corduliidae
- E *Diphebia coerulescens*, Amphipterygidae
- F *Synlestes weyersii tillyardi*, Synlestidae
- G *Telephlebia godeffroyi*, Aeshnidae
- H *Austrolestes cingulatus*, Lestidae
- I *Nososticta solida*, Protoneuridae
- J *Austrocnemis splendida*, Coenagrionidae
- K *Pseudagrion aureofrons*, Coenagrionidae

(All magnified 1.2 times, except J, which is magnified 1.8 times)

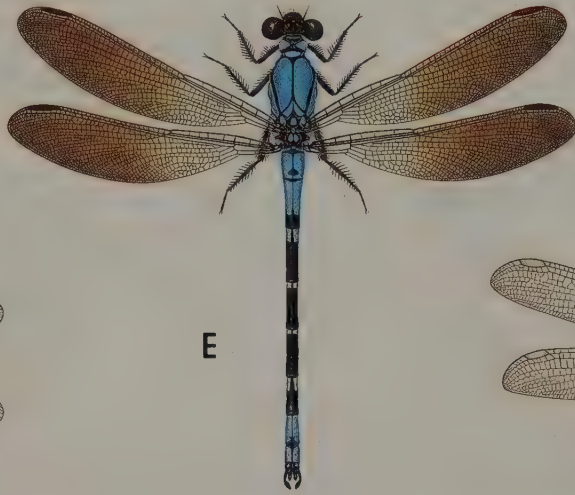


PLATE 2

MANTODEA

- A *Tenodera australasiae*, ♀, Mantidae

BLATTODEA

- B *Polyzosteria viridissima*, ♂, Blattidae
C *Anamesia polyzona*, ♂, Blattidae
D *Ellipsidion magnificum*, ♀, Blattellidae

DERMAPTERA

- E *Apachyus peterseni*, ♂, Labiduridae

ORTHOPTERA

- F *Gastrimargus musicus*, ♂, Acrididae
G *Froggattina australis*, ♂, Acrididae
H *Monistria pustulifera*, ♂, Pyrgomorphidae
I *Moraba virgo*, ♀, Eumastacidae
J *Kosciuscola tristis*, ♂ (dark and pale phases), Acrididae
K *Alectoria superba*, ♀, Tettigoniidae
L *Acripeza reticulata*, ♀, Tettigoniidae

(All magnified 1.2 times)

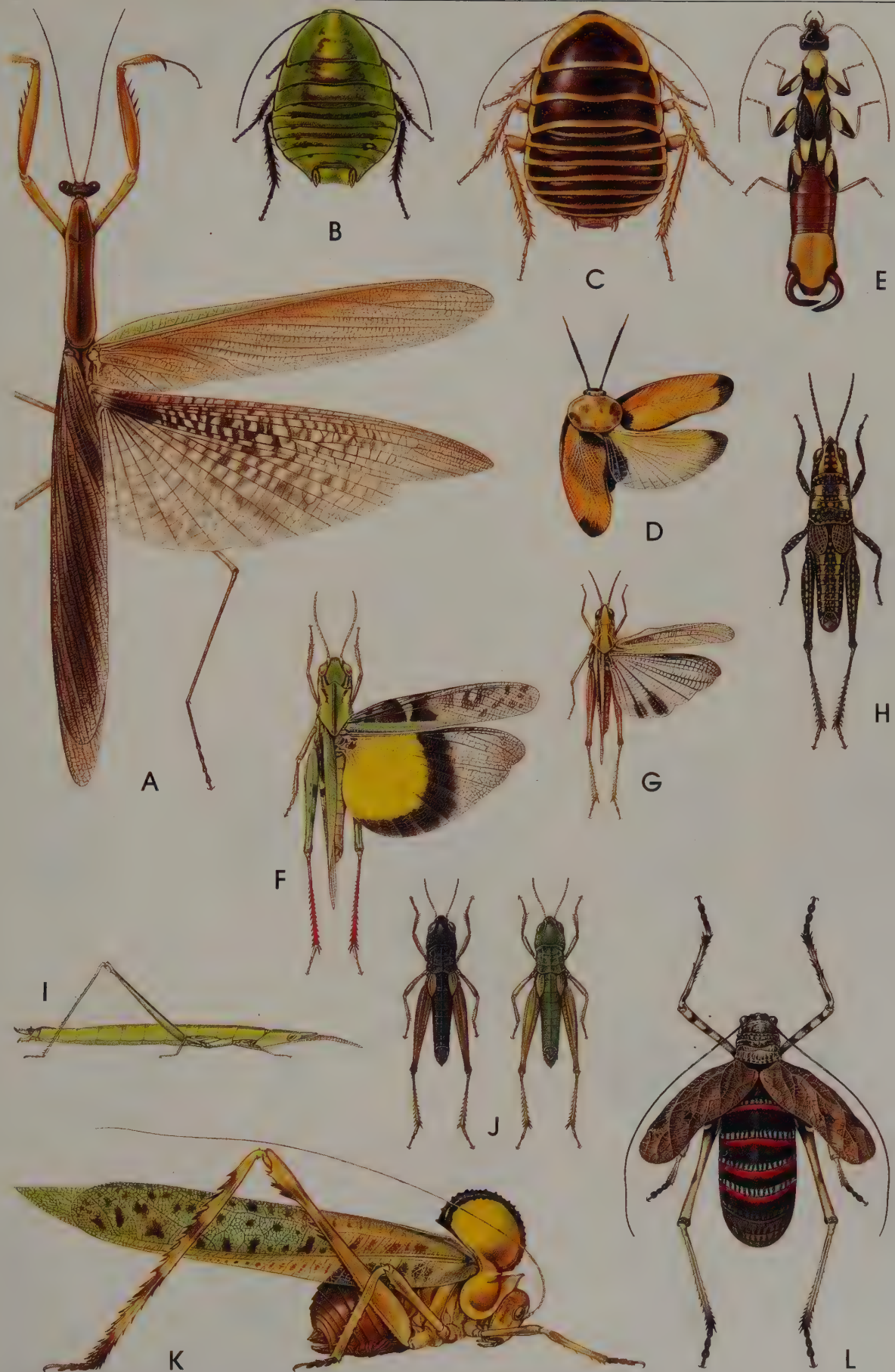


PLATE 3

HEMIPTERA

AUCHENORRHYNCHA

- A *Desudaba danae*, Fulgoridae (x 1.2)
- B *Achilus flammeus*, Achilidae (x 1.8)
- C *Siphanta acuta*, Flatidae (x 1.8)
- D *Platybrachys leucostigma*, Eurybrachyidae (x 1.8)
- E *Gelastopsis insignis*, Eurybrachyidae (x 1.8)
- F *Eoscarta carnifex*, Cercopidae (x 1.8)
- G *Cicadetta melete*, Cicadidae (x 1.2)
- H *Eurymelops bicolor*, Eurymelidae (x 1.2)

HETEROPTERA

- I *Ectomocoris decoratus*, Reduviidae (x 1.8)
- J *Ectomocoris ornatus*, Reduviidae (x 1.2)
- K *Ptilocnemus femoratus*, Reduviidae (x 2.4)
- L *Morna florens*, Pentatomidae (x 1.8)
- M *Poecilometis armatus*, Pentatomidae (x 1.2)
- N *Catacanthus nigripes*, Pentatomidae (x 1.2)
- O *Commius elegans*, Pentatomidae (x 1.8)
- P *Tectocoris diophthalmus*, Scutelleridae (x 1.2)
- Q *Scutiphora pedicellata*, Scutelleridae (x 1.8)
- R *Stauralia chloracantha*, Acanthosomatidae (x 1.8)
- S *Oncomeris* sp., Tessaratomidae (New Guinea) (x 1.2)
- T *Peltocopta crassiventris*, ♂, Tessaratomidae (x 1.2)
- U *Lampromicra senator*, Scutelleridae (x 1.8)
- V *Melanerythrus mactans*, Lygaeidae (x 1.8)
- W *Spilostethus hospes*, Lygaeidae (x 1.8)
- X *Dysdercus cingulatus*, Pyrrhocoridae (x 1.2)
- Y *Physopelta gutta*, Largidae (x 1.2)
- Z *Aulacosternum nigrorubrum*, Coreidae (x 1.8)

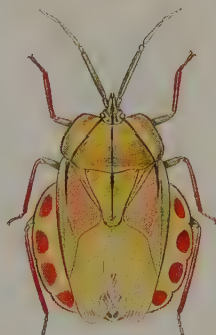
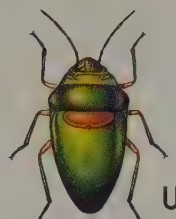
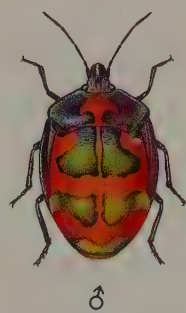
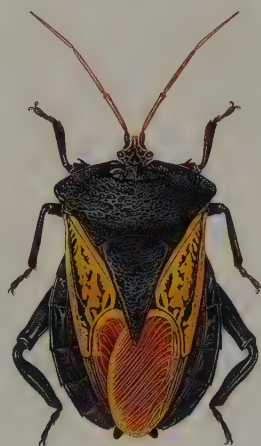
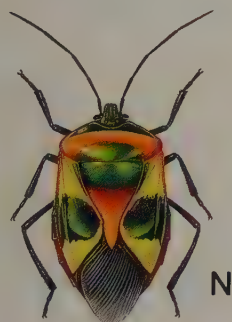
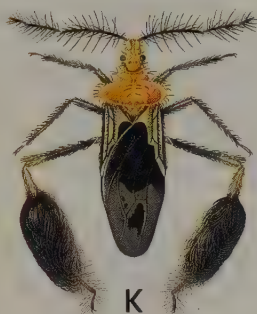
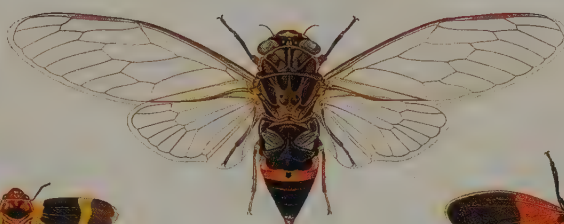


PLATE 4

COLEOPTERA

- A *Megacephala australis*, Carabidae-Cicindelinae
- B *Calosoma schayeri*, Carabidae-Carabinae
- C *Prophanes mastersi*, Tenebrionidae-Tenebrioninae
- D *Anoplognathus aureus*, Scarabaeidae-Rutelinae
- E *Anoplognathus smaragdinus*, Scarabaeidae-Rutelinae
- F *Anoplognathus smaragdinus*, colour variety
- G *Rhipidocerus australasiae*, Cerambycidae-Prioninae
- H *Paracalais gibboni*, Elateridae
- I *Eurhamphus fasciculatus*, Curculionidae-Molytinae
- J *Rhytiphora dallasi*, Cerambycidae-Lamiinae
- K *Penthea pardalis*, Cerambycidae-Lamiinae
- L *Anoplognathus viriditarsis*, Scarabaeidae-Rutelinae
- M *Anoplostethus laetus*, colour variety, Scarabaeidae-Rutelinae
- N *Phalacrognathus muelleri*, Lucanidae
- O *Ischiopsopha yorkiana*, Scarabaeidae-Cetoniinae
- P *Eupoecila australasiae*, Scarabaeidae-Cetoniinae
- Q *Sagra papuana*, Chrysomelidae-Sagrinae
- R *Uracanthus triangularis*, Cerambycidae-Cerambycinae
- S *Carenum sumptuosum*, Carabidae-Carabinae
- T *Stigmodera gratiosa*, Buprestidae-Buprestinae
- U *Lamprima aurata*, Lucanidae
- V *Cyphogastra pistor*, Buprestidae-Buprestinae
- W *Stigmodera chevrolati*, Buprestidae-Buprestinae
- X *Stigmodera amabilis*, Buprestidae-Buprestinae
- Y *Pseudotaenia quadrisignata*, Buprestidae-Buprestinae
- Z *Stigmodera alternata*, Buprestidae-Buprestinae
- ZA *Calodema regalis*, Buprestidae-Buprestinae

(All magnified 1.2 times)

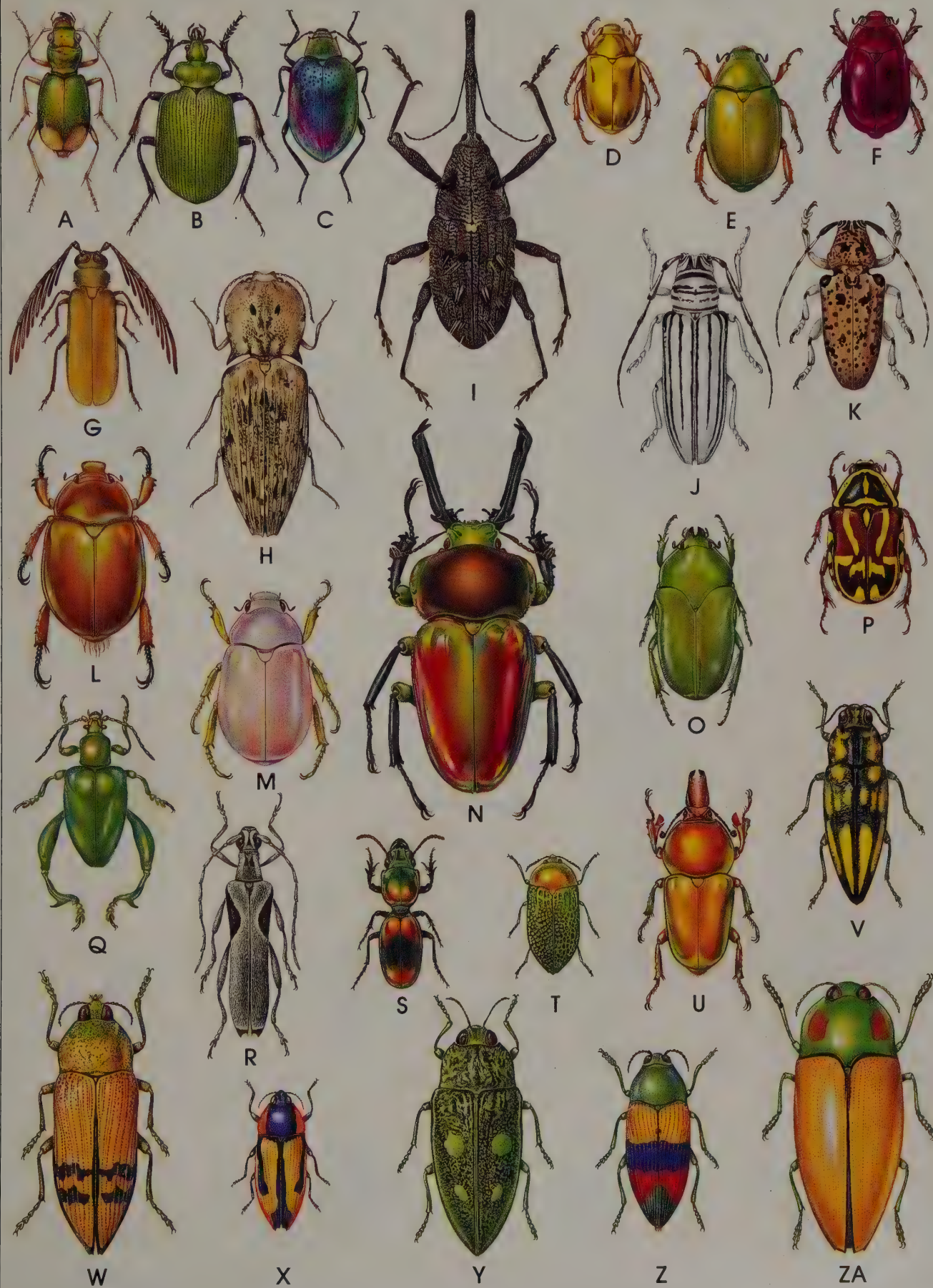


PLATE 5

COLEOPTERA

- A *Chrysolopus spectabilis*, Curculionidae-Aterpinae, blue form
- B *Episcaphula pictipennis*, Erotylidae
- C *Spilopyra sumptuosa*, Chrysomelidae-Eumolpinae
- D *Lemodes mastersi*, Anthicidae
- E *Apterotheca besti*, Tenebrionidae-Coelometopinae
- F *Rupilia ruficollis*, Chrysomelidae-Galerucinae
- G *Encymon immaculatus*, Endomychidae
- H *Pedilophorus gemmatus*, Byrrhidae
- I *Diphucephala colaspoides*, Scarabaeidae-Melolonthinae
- J *Paederus cruenticollis*, Staphylinidae-Paederinae

(A magnified 1.2 times, B-J magnified 3.6 times)

DIPTERA

- K *Clytocosmus helmsi*, Tipulidae
- L *Lamprogaster violacea*, Platystomatidae
- M *Laphria hirta*, Asilidae
- N *Scaptia auriflua*, ♂, Tabanidae
- O *Formosia speciosa*, Tachinidae
- P *Rutilia formosa*, Tachinidae

(All magnified 1.2 times)

HYMENOPTERA

- Q *Exeirus lateritius*, ♀, Sphecidae-Nyssoninae
- R *Diamma bicolor*, ♀, Tiphidae-Thynninae
- S *Myrmecia nigrocincta*, worker, Formicidae-Myrmeciinae
- T *Turneromyia* sp., ♀, Pompilidae
- U *Lestis aeratus* Smith, ♂, Anthophoridae-Xylocopinae
- V *Stilbum cyanurum*, ♀, Chrysididae

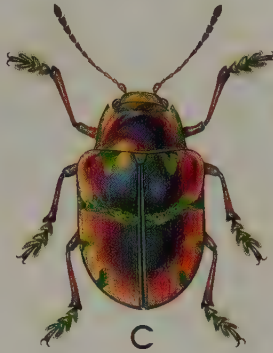
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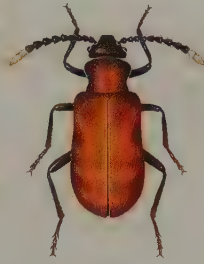
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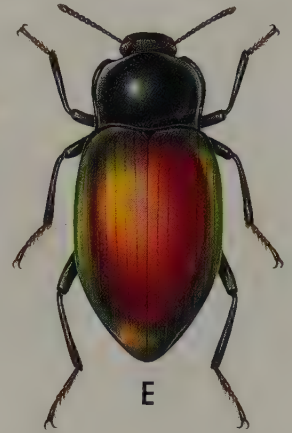
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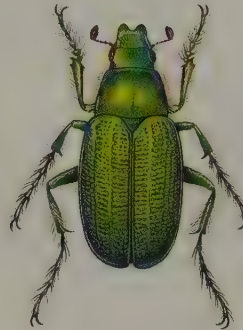
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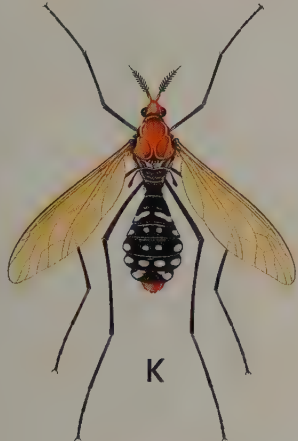
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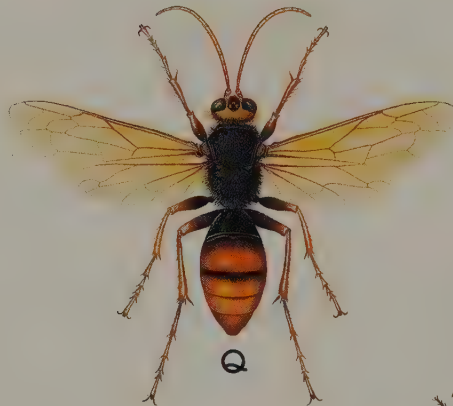
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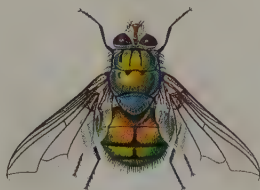
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U



V

PLATE 6

BATESIAN MIMICRY

The examples (all approximately 1.2 times life size) are mostly of group rather than specific resemblances. In Lycidae and Braconidae the models are presumably distasteful; in the other Hymenoptera illustrated they have a powerful sting.

- A *Metriorrhynchus rhipidius*, Coleoptera-Lycidae (model)
- B *Eroschema poweri*, Coleoptera-Cerambycidae (mimic)
- C *Tmesidera rufipennis*, Coleoptera-Meloidae (mimic)
- D *Rhinotia haemoptera*, Coleoptera-Belidae (mimic)
- E *Stigmodera nasuta*, Coleoptera-Buprestidae (mimic)
- F *Snellenia lineata*, Lepidoptera-Oecophoridae (mimic)

- G *Hyleoides concinna*, Hymenoptera-Colletidae, a Müllerian mimic of many stinging wasps (model)
- H *Codula limbipennis*, Diptera-Asilidae (mimic)
- I *Syndipnomyia auricincta*, Diptera-Stratiomyidae (mimic)
- J *Hesthesis variegata*, Coleoptera-Cerambycidae (mimic)

- K *Pseudabispa ephippioides*, Hymenoptera-Vespidae (model)
- L *Chrysopogon crabroniformis*, Diptera-Asilidae (mimic)
- M *Hesthesis ferruginea*, Coleoptera-Cerambycidae (group mimic)

- N *Australozethus* sp., Hymenoptera-Vespidae (model)
- O *Hesthesis cingulata*, Coleoptera-Cerambycidae (mimic)

- P *Williamsita smithiensis*, Hymenoptera-Sphecidae (model)
- Q *Conops* sp., Diptera-Conopidae (mimic)

- R *Sceliphron laetum*, Hymenoptera-Sphecidae (model)
- S *Systropus flavoornatus*, Diptera-Bombyliidae (mimic)

- T *Paralastor constrictus*, Hymenoptera-Vespidae (model)
- U *Ceriodes macleayi*, Diptera-Syrphidae (mimic)

- V *Auplopus* sp., Hymenoptera-Pompilidae (model)
- W *Agapophytus flavicornis*, Diptera-Therevidae (mimic)

- X *Clitemnestra* sp., Hymenoptera-Sphecidae (model)
- Y *Leucopsina odyneroides*, Diptera-Acroceridae (mimic)

- Z *Pycnobracon* sp., Hymenoptera-Braconidae (model)
- ZA *Plecia* sp., Diptera-Bibionidae (apparent mimic)

- ZB A braconine wasp, Hymenoptera-Braconidae (model)
- ZC *Hestiochora tricolor*, Lepidoptera-Zygaenidae (apparent mimic)
- ZD *Coracistis erythrocorma*, Lepidoptera-Oecophoridae (apparent mimic)



A



B



C



D



E



F



G



H



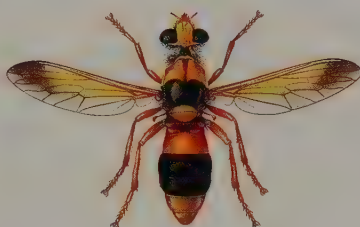
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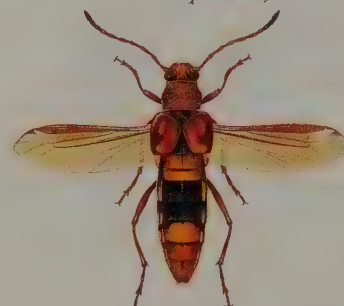
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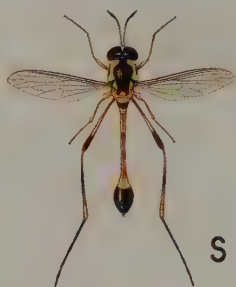
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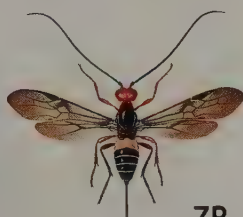
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ZB



ZC



ZD

PLATE 7

LEPIDOPTERA

- A *Macarostola formosa*, Gracillariidae
- B *Wingia rectiorella*, Oecophoridae
- C *Heliodines princeps*, Heliodinidae
- D *Carmenta chrysophanes*, Sesiidae
- E *Snellenia lineata*, Oecophoridae
- F *Macarangela leucochrysa*, Yponomeutidae
- G *Oenistis entella*, Arctiidae
- H *Telecrates laetiorella*, Oecophoridae
- I *Nemophora sparsella*, Adelidae
- J *Comana corones*, Limacodidae
- K *Dichomeris ochreoviridella*, Gelechiidae
- L *Atteva niphocosma*, Yponomeutidae
- M *Stemorrhages marthesiusalis*, Pyralidae
- N *Pollanisus trimaculus*, Zygaenidae

(Each scale = 2 mm)

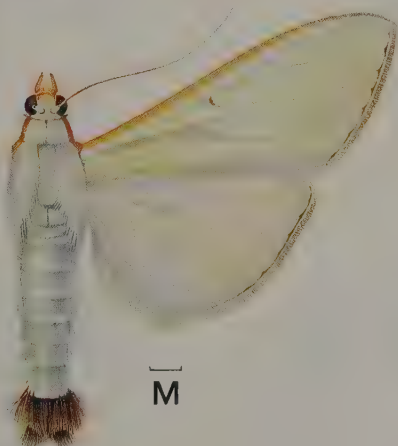
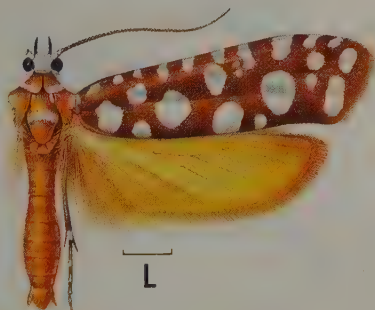
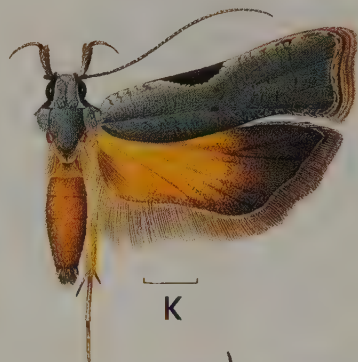
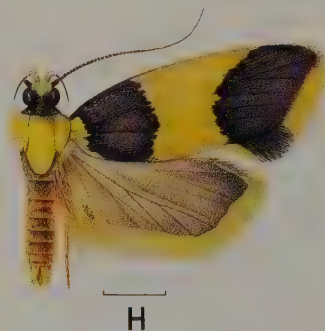
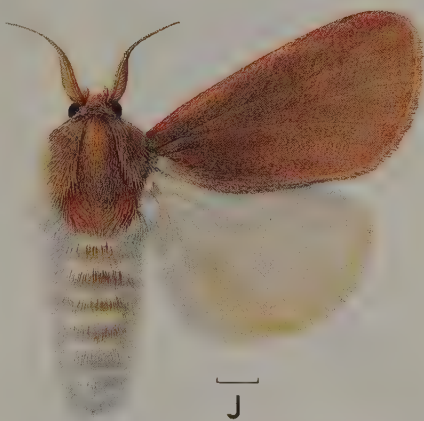
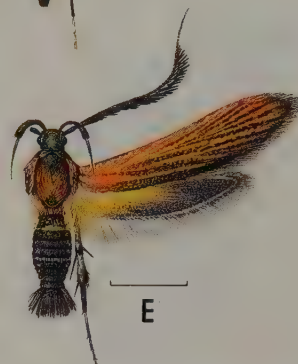
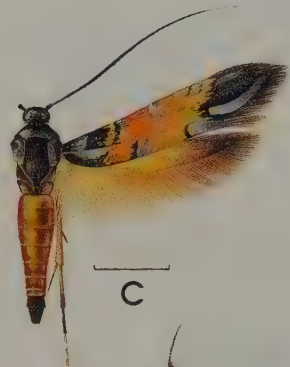
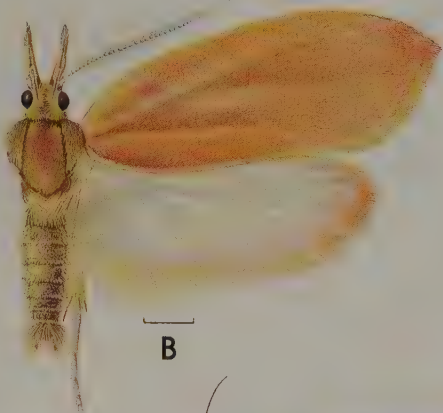
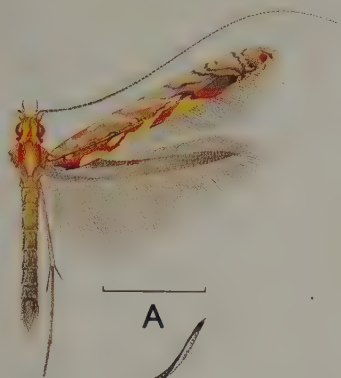
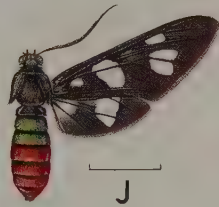
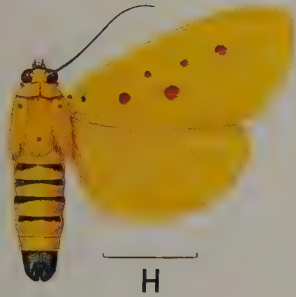
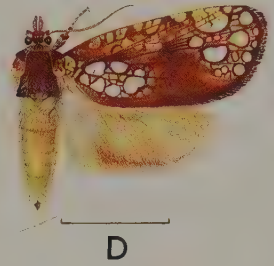
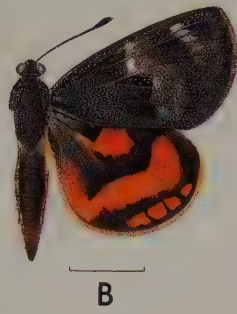


PLATE 8

LEPIDOPTERA

- A *Aenetus eximia*, ♂, Hepialidae
- B *Synemon magnifica*, Castniidae
- C *Hypochrysops apelles*, Lycaenidae
- D *Dudgeonea actinias*, Dudgeoneidae
- E *Ogyris genoveva*, ♂, Lycaenidae
- F *Coscinocera hercules*, ♂, Saturniidae
- G *Cethosia cydippe*, Nymphalidae
- H *Agape chloropyga*, Aganaiidae
- I *Alcides zodiaca*, Uraniidae
- J *Euchromia creusa*, Arctiidae
- K *Papilio ulysses*, Papilionidae
- L *Anisozyga pieroides*, Geometridae
- M *Hecatesia fenestrata*, Noctuidae
- N *Euschemon rafflesia*, Hesperidae

(Each scale = 10 mm)



Diplura

B. CONDÉ and J. PAGÉS

Small to large, narrow-bodied hexapods, mostly unpigmented (except caudal segments of japygids); eyes absent; antennae moniliform, with intrinsic muscles in the flagellar segments; thorax usually weakly developed; legs 5-segmented; abdomen 10-segmented, with styles and exsertile vesicles on at least some of the segments, gonopore between 8 and 9; cerci variously developed. Larval development epimorphic.

This is a cosmopolitan order of about 800 species. They are mainly found in damp soil under logs or stones, and are the most insect-like of the entognathous orders. Size and form vary and range from symphylan-like campodeids less than 5 mm long to dermapteran-like *Heterojapyx* up to 50 mm in length. The skeletal anatomy of *Heterojapyx* has been described by Snodgrass (1952), and the Australian species by Womersley (1939, 1945), Tillyard (1924), Silvestri (1947) and Pagés (1952).

Anatomy of Adult

Head (Fig. 13.1). An egg-shaped, prognathous capsule, with indications of cleavage lines dorsally. Eyes absent. Antennae moniliform, often with *trichobothria* on some segments. Ventral surface almost totally enclosed by fusion of the cranial folds with the lateral margins of the wide labium over almost its whole length, so that only the tips of the mandibles and maxillae visible anteriorly. The fulcrum, as in Collembola and presumably in Protura, corresponds with the posterior tentorial arms of the Insecta (Manton 1964). Apart from the mobility of the mandibles associated with the entognathy, the most striking features of the mouth-parts are the presence of a prostheca (cf. Ephemeroptera) on the mandibles in all families except japygids, and the marked reduction of both maxillary and labial palps. There is a large, trilobed hypopharynx.

Thorax. Tergal and sternal plates well developed. Two

to 4 laterally placed thoracic spiracles (2 in Parajapygidae, 3 in Campodeidae and Projapygidae, 4 in Japygidae and Heterojapygidae). Legs usually short, pretarsus with a pair of claws and sometimes also a median claw.

Abdomen. Ten-segmented, with well-developed terga and sterna. S2–7 usually with small, lateral styles and exsertile vesicles (Fig. 13.2); the arrangement on S1 varies within families; S1 with median, glandular organ in many Japygidae. Gonopore in both sexes in a pouch

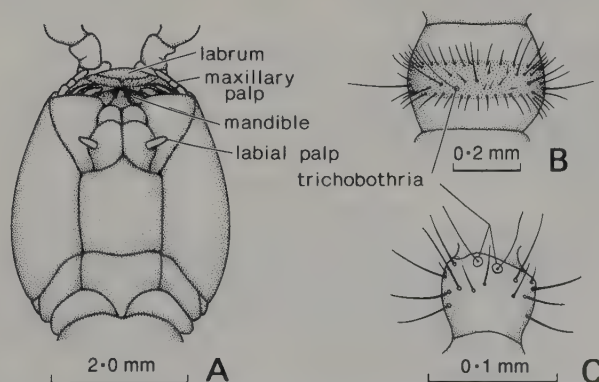


Fig. 13.1 A, head of *Heterojapyx evansi*, Heterojapygidae, ventral; B, 7th segment of right antenna of *H. evansi*, dorsal; C, 6th segment of right antenna of *Metriocampa* sp., Campodeidae, dorsal.

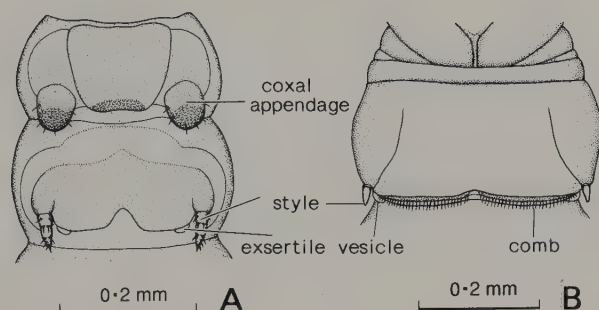


Fig. 13.2 Abdominal segments, ventral: A, 1st and 2nd of male *Metriocampa* sp.; B, 1st of *Heterojapyx evansi*.

behind S8; usually genital armature absent, although male japygids have a pair of short appendages; anus terminal. The cerci differ markedly in the three major groups. In Campodeidae they are long, filiform, many-segmented, and resemble the antennae; in Projapygidae, Anajapygidae and Procampodeidae they are shorter annulate; these families possess a mass of glandular cells in the abdomen, at the base of the cerci, but only the first two families have cerci provided with a duct opening at the apex; in Japygidae they are reduced to a pair of strong, 1-segmented, pigmented forceps, which are held open by elastic tension at rest and closed by strong muscles. There are 7 pairs of abdominal spiracles in Projapygidae and Japygidae, but none in Campodeidae.

Internal Anatomy. Alimentary canal simple; Malpighian tubules reduced to 6 small papillae or absent. Usually 8 discrete abdominal ganglia in japygids, but only 7 in other Diplura. The tracheal systems of opposite sides apparently do not anastomose. Seven, apparently metamERICALLY arranged pairs of ovarioles in *Japyx* and *Heterojapyx*, but only a single pair in campodeids; germaria apical; the genital tubes fuse to form a median duct in both sexes.

Immature Stages

The egg is heavily yolked, cleavage is meroblastic, there is no amnion, and the embryo has a large dorsal organ similar to that of Symphyla and Collembola. Post-embryonic development is epimorphic, with little change, except for an increase in the number of antennal segments in some groups, progressive development of chaetotaxy, and sometimes changes in the cerci. Development is slow, and moulting continues throughout life, about 30 ecdyses having been observed in *Campodea*. Sexual maturity appears to be reached at the stage when the chaetotaxy is complete (Wygodzinsky 1987).

Biology

The less aggressive Diplura, like the Symphyla, often occur in aggregations or small 'colonies'. A few species have been found in ants' nests and termitaria, but the association appears to be casual. *Campodea* has moderately effective legs; the legs are stronger in japygids; these can move through cracks in the soil either by a worm-like action of their thoracic and abdominal segments or by digging burrows with the maxillae. Campodeids seem mostly to be herbivorous, as is *Parajapyx*; other Diplura are generally carnivorous and depending on their size, prey are caught either with the maxillae or with the cerci; *Heterojapyx* has been observed to wait buried in the soil with only the forceps on the surface, ready to seize any small arthropod that comes in contact with them.

Fertilisation, where known, is by means of a spermatophore attached to the substrate by a short stalk. The smooth, spherical eggs are laid in clumps, often attached by a stalk, within rotting vegetation or in cracks in the soil. Female japygids guard their eggs and young larvae. The young members of a family group of *Heterojapyx* have been observed to devour the female parent, and cannibalism also occurs in the older stages in captivity. Isolated adults have been kept alive for more than a year.

CLASSIFICATION

Order DIPLURA

(31 Australian spp.)

- | | | |
|---------------------|------------------------|----------------------|
| 1. Campodeidae (10) | Anajapygidae (0) | Dinjapygidae (0) |
| Procampodeidae (0) | 3. Japygidae (12) | Evalljapygidae (0) |
| 2. Projapygidae (2) | 4. Heterojapygidae (4) | 5. Parajapygidae (3) |

Since Paclt's (1957) classification of Diplura, many changes have taken place, especially in japygids where all previous subfamilies are now given family rank. Dinjapygidae and Evalljapygidae are known only from

the New World and it is unlikely they will be found in Australia. However, it is not unlikely that one or more species of Anajapygidae and Procampodeidae might be discovered here.

Key to the Families of Diplura

- | | |
|--|---------------------|
| 1. Cerci multisegmented; mandible with a prostheca | 2 |
| Cerci 1-segmented, forcipate; mandible without prostheca | 5 |
| 2(1). S1 with 2 pairs of appendages; trichobothria absent on segment 3 of antenna; cerci rather short, last joint modified into a short retractible tubular outlet of the abdominal glands | 3 |
| S1 with one pair or no appendages; trichobothria present on segment 3 of antenna; cerci rather long, last joint entire, not modified | 4 |
| 3(2). Trichobothria on segments 4–22 of antenna; labial palps long, cylindrical and with numerous setae | Projapygidae |
| Trichobothria on segments 5–12 of antenna; labial palps reduced to mere knobs with few setae | Anajapygidae |
| 4(2). Trichobothria on segments 3–6 of antenna; S1 with a pair of setose appendages | Campodeidae |

- Trichobothria on segments 3–7 of antenna; S1 without appendages Procampodeidae
- 5(1). No trichobothria on antenna; labial palp absent but a pair of robust setae in their place; S2–3 with one pair of circular vesicles; 2 pairs of thoracic spiracles **Parajapygidae**
- Trichobothria present on antennal segment 4 and a number of more distal ones, labial palps present; S1–7 with minute membranous vesicles; 4 pairs of thoracic spiracles 6
- 6(5). Trichobothria only on segments 4–6 of antenna; pretarsus without empodium on ventral side of the 2 lateral claws **Japygidae**
- Trichobothria present on more than 3 segments of antenna; pretarsus with conical empodium on ventral side of the 2 lateral claws **Heterojapygidae**

1. Projapygidae (Fig. 13.3c). Small, primitive species, which can be distinguished from campodeids by their larger heads, more japygid-like build, and shorter, thicker cerci carrying the ducts of abdominal silk glands. The two known Australian species of *Symphylurinus* appear to be rare, *S. swani* from North Qld, and an undescribed species from W.A. (Bornemissza 1967).

2. Campodeidae (Fig. 13.3b). The few, known Australian species are probably only a minor part of the continent's actual campodeid fauna. The pantropical subfamily Lepidocampinae, which forms about 90% of the Papua New Guinea fauna should be searched for in Qld.

The ubiquitous subfamily CAMPODEINAE is represented by four genera. Three subgenera of *Campodea* are present. *Campodea* (*Campodea*) *fragilis* is subcosmopolitan. *C. (Monocampa) tonnoiri*, which belongs to the *devoniensis-quilisi* complex, was found in an Adelaide garden with *C. (C.) fragilis* and possibly is introduced.

Indocampa, a typically Oriental subgenus of *Campodea*, is known from Madagascar to Polynesia; *C. (I.) tillyardii* occurs in all Australian states and New Zealand, and *C. (I.) froggattii* in Tas. An unnamed species from Woody I. (near Esperance, W.A.) is allied to *C. (I.) novaecaledoniae*, the only species of *Indocampa* known from a cave. *C. waterhousei* from Sydney, N.S.W., may also belong to *Indocampa*. The three remaining genera have unusual distributions. *Campodella*, with *tiegsi* from Vic., is only known elsewhere from Natal (*clavigera*, type species) and Madagascar (*milloti*). *Austrocampa* (a subgenus of *Metriocampa*) is represented by *M. (A.) spinigera* from W.A. (Denmark and Porongorups) and its debatable subspecies *victoriense* from Vic.; there are strong spines basally and internally on the male cerci similar to spines on the cerci of female *Metriocampa* (*Tricampa*) *paradoxa* from Colorado, U.S.A. *Notocampa* has a Gondwanan distribution: South America (Chile), South Africa (Natal), Madagascar, Australia (*N. leae* from S.A., *N. westraliense* from W.A.) and New Zealand. Species of *Notocampa* are more robust and hairy than other Australian campodeids, making preliminary identification easy.

3. Japygidae. The Australian japygids are too poorly known to permit a correct generic assignment of the 13 described species. Paclt's (1957) generic classification is unsatisfactory and cannot be accepted entirely. *Japygianus* (monotypic for *J. wheeleri*, Qld) with its short, squat cerci and long abdominal segment 10 is the most distinctive. *Notojapyx* (endemic to Australia with *N. mjobergi*, *N. tillyardi* and its subspecies *pagesi*) is relatively well characterised by its 26-segmented antenna and its maxillae with only 4 pectinate laminae. Among the 10 remaining species some may belong in *Indjapyx* but certainly none in *Burmjapyx* or *Teljapyx*, as defined by Silvestri (1947).

4. Heterojapygidae (Fig. 13.3a). *Heterojapyx* is the most distinctive genus of japygids by reason of the remarkable robustness of the species, four of which are found in the mountains of eastern Australia (Vic., N.S.W., A.C.T.). The genus has also been recorded from New Zealand, Madagascar, Pamir and Tibet.

5. Parajapygidae (Fig. 13.3d). All the species of the cosmopolitan genus *Parajapyx* are small (about 3–5 mm long); and 3 species are known widely scattered in Qld, W.A. and S.A.

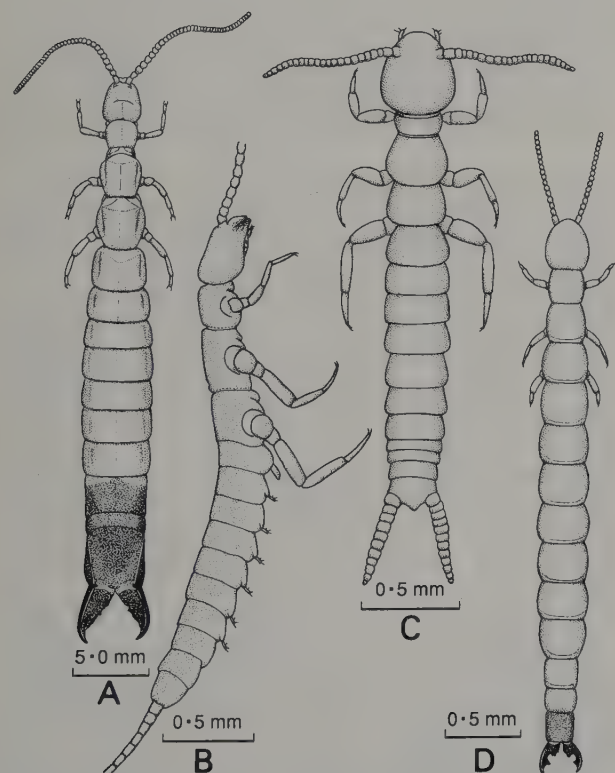


Fig. 13.3 Diplura (setae omitted): A, *Heterojapyx evansi*, Heterojapygidae, dorsal; B, *Campodea* sp., Campodeidae, lateral; C, *Symphylurinus* sp., Projapygidae, dorsal; D, *Parajapyx swani*, Parajapygidae, dorsal.

[B. Rankin]

ACKNOWLEDGMENTS. Valuable comments on drafts of this chapter were provided by Ms P. Greenslade, Canberra, Australia and Dr W. W. K. Houston, Australian Biological Resources Study, Canberra, Australia.

Archaeognatha

Microcoryphia

(*Bristletails*)

J. A. L. WATSON and G. B. SMITH

Fusiform, subcylindrical, primitively wingless insects, with the ability to jump. Body with or without hypodermal pigment, bearing pigmented scales. Compound eyes large, contiguous; ocelli present; antennae elongate, flagellum filiform; mouth-parts ectognathous; mandible with a single articulation; maxillary palp long, 7-segmented; thorax strongly arched, the terga extending over pleura; styles often present on coxae; abdominal segments 2–9 with ventral styles, 1–7 generally with 1 or 2 pairs of exsertile vesicles; female with well-developed, slender ovipositor, without gonangulum; appendix dorsalis elongate, filiform, longer than filiform cerci.

This small, homogeneous and cosmopolitan order includes about 350 known species in one extinct and two living families. Previously grouped with the Thysanura (p. 275), these silverfish-like insects are characterised by their unique and ancient monocondylar mandibles (Manton 1964) (p. 148). Denis (1949), Paclt (1956), Delany (1957), Sharov (1966) and Hennig (1969) reviewed them (as part of the subclass). Womersley (1939) documented the then-known Australian fauna and Sturm (1980) reviewed *Nesomachilis*.

Anatomy of Adult

Head (Figs 14.1A–E). Hypognathous. Compound eyes large, contiguous, often colourful in life. Ocelli present, the lateral pair below anterior margin of eyes and, generally, transversely elongate. Antennae with multisegmented, elongate flagellum. Mandibles (Fig. 14.1B) long, monocondylar, apical incisor process widely separated from molar process, operating with a rolling motion. Hypopharynx (Fig. 14.1E) trilobed; lingua lying between labium and maxilla and superlinguae between maxilla and mandible. Maxilla and labium normal; maxillary palp long, protruding anteriorly, 7-segmented; labial palp short, 3-segmented. Anterior arms of tentorium discrete.

Thorax. Terga entire, strongly arched, and produced

into large lateral lobes (Fig. 14.1F). Pleura represented by one small sclerite in mesothorax, one in metathorax, and several in prothorax, covered by tergal lobes. Sterna small. Meso- and metathoracic spiracles present.

Legs. Coxa large, trochanter 2-segmented, tarsi 3- or rarely 2-segmented, the pretarsus with 2 claws. Mid and hind coxae, or hind coxae alone, often bearing styles (Fig. 14.2B), which lack muscles and are not homologous with abdominal styles. A plane of autotomy present between trochanter and femur.

Abdomen. Tapering, the contour continuous with that of thorax. Terga large, extending around side of body. Sternal region comprising a basal sternum, greatly reduced in the Meinertellidae, and posterolateral coxites (Figs 14.1G, H). Coxites 2–9 bearing large styles actuated by muscles, apparently representing reduced limbs (p. 150). Coxites 1–7 or 2–7 generally with 1 or 2 pairs of exsertile vesicles medial to the styles, often inconspicuous. Spiracles present on segments 2–8. The terminalia are described on pp. 18–20, 150.

Internal Anatomy. Alimentary canal simple; crop small, proventriculus absent; enteric caeca present; 12–20 well-developed Malpighian tubules. Salivary glands and labial kidneys present. Nervous system generalised, with 3 thoracic and 8 abdominal ganglia, the connectives

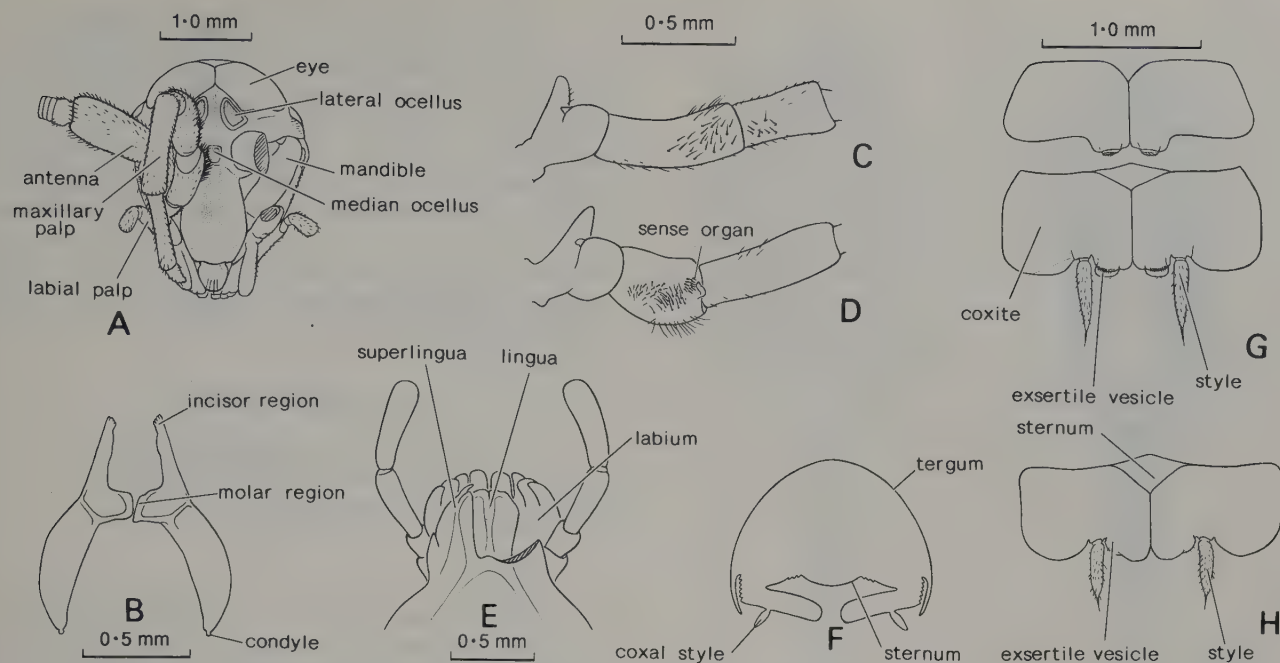


Fig. 14.1 A, head of *Allomachilis froggatti*, ♂, frontal view with left antenna and maxillary palp removed; B, mandibles of *Nesomachilis australica*; C, base of male maxillary palp of *A. froggatti*; D, same of *N. australica*; E, labium and hypopharynx of *A. froggatti* with right lateral lobe of hypopharynx removed; F, diagrammatic transverse section through thorax of *Allomachilis*; G, sternal regions of abdominal segments 1 and 2 of *N. australica* with segments separated to show sternum 2; H, same of segment 2 of *A. froggatti*. Scales and many setae omitted throughout. [M. Quick]

appearing double throughout. Tracheal system well developed, inter- or intrasegmental anastomoses faintly so. Ovaries with 7 or 8, rarely 5, panoistic ovarioles; spermatheca and accessory glands apparently lacking. Testes with 3 or 4 follicles; vas deferens of each side double, the dual channels being interconnected by several transverse tubes; median reservoir present.

Immature Stages

Eggs globular, soft and orange when first laid, conforming to crevices in which they are placed, later hardening and darkening (Delany 1957). Embryonic development typically insectan, but amniotic cavity incompletely closed. Larval development 'ametabolous', the larva closely resembling the adult. First instar larva with abdominal styles and inner series of exsertile vesicles complete; scales appearing at second ecdysis; outer series of vesicles (if present), coxal styles and gonapophyses developing progressively later. Sexual maturity attained in 8th or 9th instar in *Petrobius*.

Biology

The Archaeognatha are free living and commonly nocturnal, hiding by day under bark, in litter or in rock crevices, and coming out to feed at night; but some show diurnal activity (Sturm 1984). The diet includes algae, lichens, and vegetable debris, the tips of the mandibles serving as augers. Several species eat their exuviae, and fragments of other arthropods have been found in the gut. The everted abdominal vesicles can absorb water from moist surfaces. *Allomachilis*, like *Petrobius* in the Northern Hemisphere, lives in crannies on coastal cliffs not far

above high tide, and shows similar weak aggregation behaviour. Archaeognatha run nimbly, though not as quickly as Thysanura (pp. 276–7), and when disturbed escape by jumping, often more than 10 cm. The jumps are induced by abrupt downward flexure of the abdomen [although Manton (1972) indicated that dorsal abdominal contraction is involved], the legs and styles playing only a minor role. *Allomachilis* can also jump short distances from the surface of water. At least in *Allomachilis*, the abdominal styles appear to supplement the legs on slopes.

Reproduction is generally sexual and seasonal, and the transfer of sperm is primitive and indirect. In some machilids the male produces small droplets of sperm on a thread, which is attached to the ground and gathered by the female. The male *Petrobius maritimus* places the sperm droplet directly on the ovipositor (Sturm 1978). Meinertellidae produce stalked spermatophores with coated or uncoated sperm droplets 0.3–0.5 µm in diameter. Parthenogenesis occurs in some species. The females lay batches of 2–30 eggs, commonly about 15, placing them deeply in crevices or in holes dug by the ovipositor. One batch is laid in each instar. The eggs overwinter in diapause. Postembryonic development is slow, the larvae taking from three months to more than a year to mature. Moulting continues throughout life. Vesicles of the abdomen are glued to the substrate before ecdysis; the abdominal styli play a role in helping the insect push itself through the dorsal ecdysial slit; and the final extrication depends on the maxillary palps and legs (E. L. Smith 1970b).

Natural Enemies. Archaeognatha commonly harbour gregarine Sporozoa in the gut. They may also become

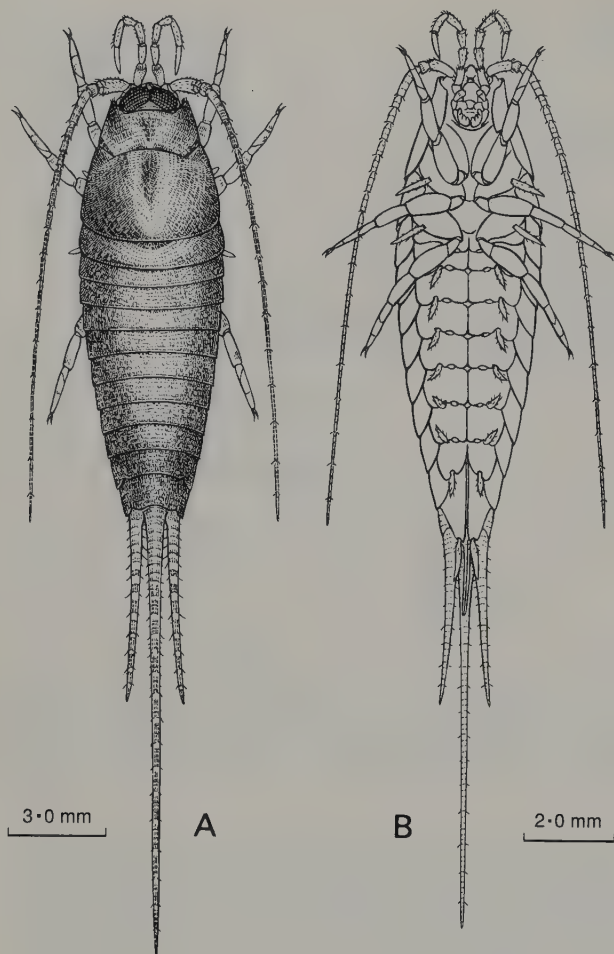


Fig. 14.2 A, *Allomachilis froggatti*, ♂, dorsal; B, *Nesomachilis australica*, ♀, ventral with vesicles exerted (scales omitted). [M. Quick]

infested with larval erythraeid mites, which attach themselves to the cuticle (Fig. 3.30). Several families of spiders are the main predators, but centipedes and carabid beetles may also feed on them.

Economic Significance. None.

Special Features of the Australian Fauna

The Australian fauna is not well known. All the species belong to the Meinertellidae, the more primitive living family, which is essentially southern (Sturm 1984); the Machilidae are found principally in the Northern Hemisphere (Denis 1949). *Allomachilis* is endemic, and *Nesomachilis* is restricted to Australia, New Zealand and Melanesia including New Guinea. *Machiloides*, to which *Nesomachilis* is closely allied, is principally South African, Madagascan and South American (Wygodzinsky 1948, 1955).

CLASSIFICATION

Order ARCHAEOGNATHA

(7 described Australian spp.)

1. Meinertellidae (7)

Machilidae (0)

1. Meinertellidae (Fig. 14.2). Distinguished by having very small abdominal sterna which protrude slightly, if at all, between the coxites, by lacking scales on the legs, scape and pedicel, and by lacking parameres; the penis is very short. The best known Australian species is *Allomachilis froggatti*, up to 15–18 mm long, which occurs on the coastal cliffs of eastern, southern and south-western Australia. It has small exsertile vesicles on abdominal segments 2–4 (Fig. 14.1H), and the 2nd segment of the male maxillary palp bears simple sensory setae (Fig. 14.1C). The other Australian species are smaller, up to 7–12 mm, have larger vesicles on abdominal segments 1–7 (Fig. 14.1G), and the male maxillary palp bears an elaborate sense organ (Fig. 14.1D). *Nesomachilis* occurs in rainforest in Qld and N.S.W. and on Lord Howe I. Male *N. queenslandica* have highly developed claspers on the fore legs; similar but less elaborate claspers occur in *N. australica* and *N. tamborina*. *Machiloides hickmani*, with dumb-bell-shaped ocelli, is recorded from beach tussocks in Tas., and allied *Machiloides* occur near Canberra and Wollongong. Undetermined Archaeognatha are known from Qld, N.S.W. and Vic.

Thysanura

Zygentoma

(*Silverfish*)

G. B. SMITH and J. A. L. WATSON

Cursorial, more or less flattened, primitively wingless insects. Body scaled or bare, with or without pigment. Compound eyes reduced or absent, never contiguous; ocelli absent except in Lepidothrichidae; antennae elongate, flagellum filiform; mouth-parts ectognathous; mandible dicondylar; maxillary palp 5-segmented; thorax not strongly arched, pleura exposed; styles present at most on abdominal segments 2–9, commonly less; 2–7 occasionally with exsertile vesicles; female with well-developed, slender ovipositor; cerci and appendix dorsalis filamentous, generally elongate and subequal in length, sometimes short, cerci strongly diverging from body axis.

This small, cosmopolitan order includes some 370 species in four living families. It is more diverse than the Archaeognatha, structurally and ecologically. Many species are inquiline, and those living with humans are familiar insects of some economic importance.

Denis (1949), Paclt (1956), Delany (1957) and Sharov (1966) discussed the Apterygota, including Thysanura, and Womersley (1939) reviewed the Australian fauna.

Anatomy of Adult

Head (Fig. 15.1A). Hypognathous, but more prognathous than in Archaeognatha. Compound eyes reduced, the component ommatidia somewhat isolated, or absent. Median and lateral ocelli present in the extralimital family Lepidothrichidae, reduced to median frontal organ in Lepismatidae, otherwise absent. Antennae long. Mandibles dicondylar (Fig. 15.1B), biting transversely as in ectognathous Pterygota; molar and incisor regions contiguous. Hypopharynx simple. Maxilla and labium of generalised form, the maxillary palp 5-segmented, the last segment sometimes secondarily subdivided; labial palp shorter, 4-segmented. Anterior arms of tentorium sometimes fused into large central plate, approaching the condition found in orthopteroids.

Thorax (Figs 15.1C–E). Terga entire, not usually strongly arched, sometimes produced laterally into lobes. Pleural region with 3 small sclerites. Sterna generally small, but produced into large posterior lobe in Lepismatidae (Fig. 15.2C). Mesothoracic spiracles sometimes appearing prothoracic, metathoracic spiracles normal.

Legs. Coxa large, flattened (Fig. 15.1C), trochanter simple, tarsi 2–5-segmented, the pretarsus bearing 2 lateral and a variable median claw. Plane of autotomy present between trochanter and femur.

Abdomen. Tapering, rarely much narrower than thorax. Terga less arched than in Archaeognatha. Sternal region in Lepidothrichidae and some Nicoletiidae divided into basal sternum and lateral coxites, otherwise fused into single 'sternum' (Figs 15.1F, G). Abdominal styles variously distributed, at most on segments 2–9, commonly on 7–9, occasionally absent. A single pair of exsertile vesicles on segments 2–7 in lepidothrichids and some nicoletiids, otherwise reduced, and absent in Lepismatidae and the extralimital family Maindroniidae. Spiracles present on segments 1–8. The terminalia are described on pp. 18–20, 150.

Internal Anatomy. Alimentary canal simple; crop well developed; proventriculus absent in Lepidothrichidae

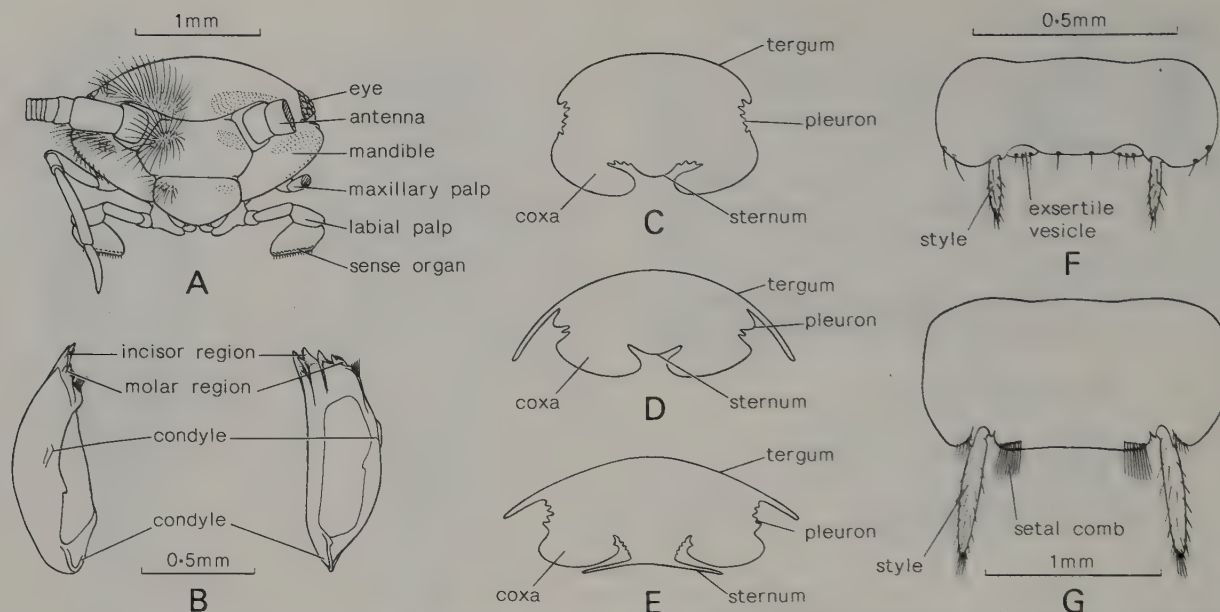


Fig. 15.1 A, head of *Ctenolepisma* sp., frontal view with left antenna and maxillary palp removed; B, mandibles of *Ct. longicaudata*, upper and inner aspects; C, diagrammatic transverse section through thorax of *Nicoletia*; D, same of *Atopatelura*; E, same of *Lepismodes*; F, abdominal 'sternum' 6 of *Atopatelura hartmeyer*; G, abdominal 'sternum' 7 of *Ctenolepisma* sp. Scales and many setae omitted throughout. [M. Quick]

and Nicoletiinae (Nicoletiidae), reduced in Atelurinae (Nicoletiidae), well developed in Lepismatidae; generally 4–8 Malpighian tubules. Salivary glands and labial kidneys present. Nervous system much as in Archaeognatha (p. 272). Tracheal system lacking large longitudinal trunks, but intra- and intersegmental anastomoses present. Ovaries with 7 panoistic ovarioles in Lepidothrichidae, 2–5 in other families; spermatheca and accessory glands present. Testes with 2–7 follicles in lepismatids and numerous follicles in lepidothrichids; male tract often highly modified for production of spermatophores.

Immature Stages

Lepismatid eggs pale brown, oval, but often distorted, as they harden and conform to the shape of the substrate. *Nicoletia* eggs pale grey, not attached to substrate. Embryonic development as in Archaeognatha (p. 273), the amnion closing except for a small pore. Frontal egg-tooth present in 1st instar, as are traces of separate cephalic tergites (Sharov 1966). Larval development much as in Archaeognatha (p. 273). Scales appear at third ecdysis; abdominal styles incomplete in 1st instar lepismatids, appearing progressively during larval and adult life; both styles and vesicles complete in newly-hatched *Nicoletia*. Sexual maturity attained between 10th and 14th instar in lepismatids (Delany 1957).

Biology

Most Thysanura are free living, and all are extremely agile. The Lepidothrichidae and most Lepismatidae are cryptozoic, living under bark or litter, but some silverfish can withstand considerable desiccation. *Lepismodes inquilinus* (= *Thermobia domestica*) and *Ctenolepisma*

longicaudata can absorb water from subsaturated atmospheres, through the highly convoluted rectal wall (Beament *et al.* 1964; Noble-Nesbitt 1970). An undetermined Australian desert species of *Acrotelsella* may have these faculties well developed, for it runs on open ground by day, pausing periodically to gyrate the elevated end of the abdomen. Nicoletiinae are principally subterranean or cavernicolous, and are vegetarian, although *Nicoletia phytophila* will eat its shed skin, and may eat its own eggs. Silverfish are otherwise omnivorous, and some can secrete an intrinsic cellulase (cf. p. 57). The Atelurinae include the smallest Thysanura, and are inquilines in nests of ants and termites, as are a few lepismatids. Some dozen species of silverfish live in association with vertebrates, most commonly with man.

Reproduction is generally sexual, although *Nicoletia phytophila* can reproduce parthenogenetically (Picchi 1972). As in the Archaeognatha, transfer of sperm is indirect, the male placing a flask-shaped spermatophore on the ground, the female picking it up and transferring its contents to the spermatheca. Nicoletiids package the sperm into mucous pellets, called spermatolophids, which are, in turn, packaged into spermatophores (Wygodzinsky 1958). Female lepismatids mate and lay one batch of eggs in each instar, whereas some nicoletiids lay individual eggs over much of it. The eggs hatch in 10–60 days. Postembryonic development may be slow, but larvae of *Lepismodes* reach sexual maturity in 2–3 months. Moulting continues throughout the long adult life of up to 4 years, and the reproductive potential is great.

Natural Enemies. Many species of Thysanura harbour gregarine Sporozoa. The primitive Mengeidae (STRP) parasitise lepismatids. Meloid beetle larvae have been

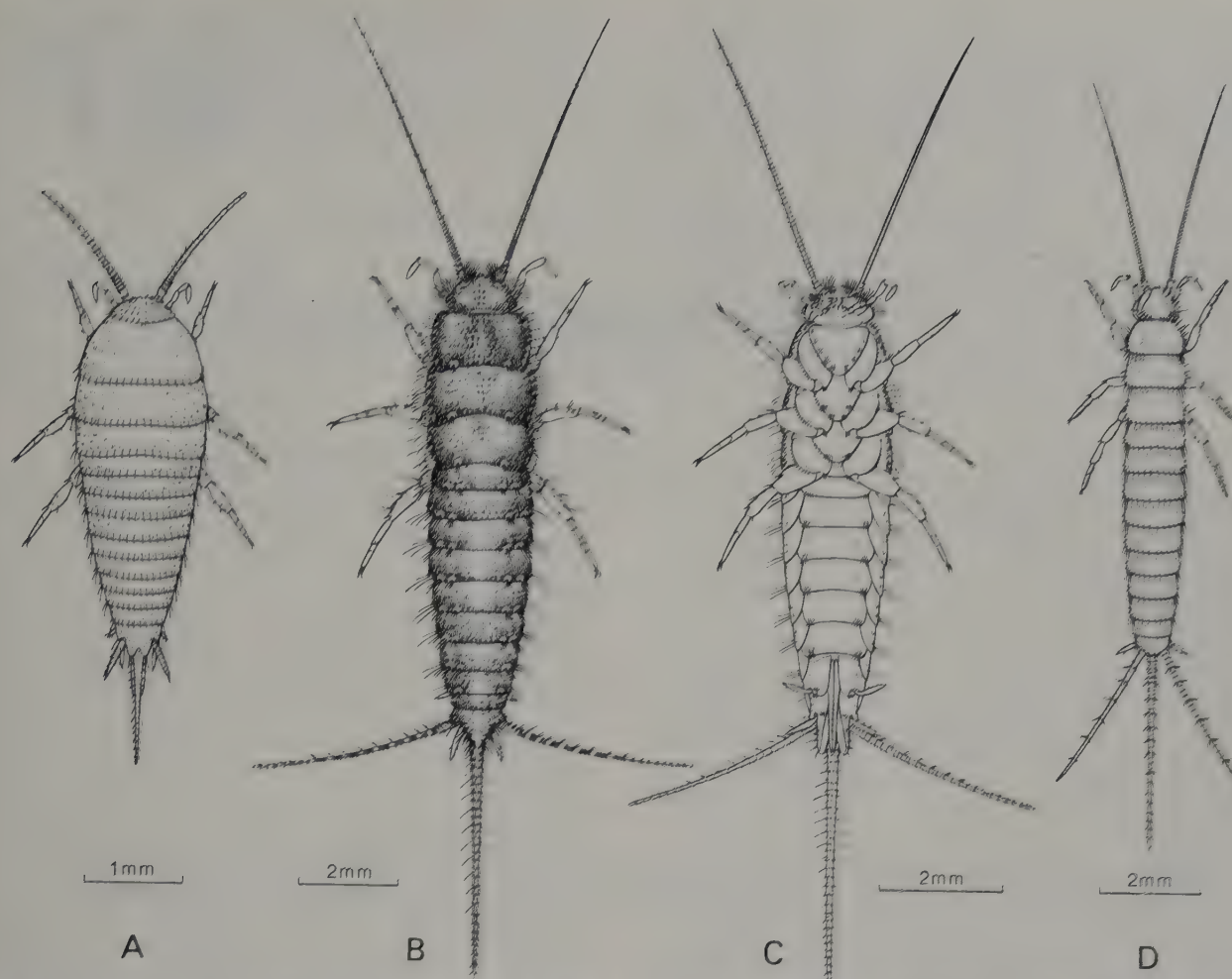


Fig. 15.2 A, *Atopatelura michaelsoni*, Nicoletiidae-Atelurinae, ♀ dorsal; B, C, *Acrotelsella devriesiana*, Lepismatidae, ♂ dorsal and ♀ ventral (scales omitted); D, *Trinemura excelsa*, Nicoletiidae-Nicoletinae, ♂ dorsal. [M. Quick]

found attached to specimens of *Trinemura excelsa*, but it is not known if they harm their host. As with the Archaeognatha, the principal predators appear to be spiders.

Economic Significance. A few nicoletiids are plant pests, and various lepismatids are pests in human habitations, where they feed on paper, glues, sizings and scraps; none is known to transmit disease. Six pest species are known from Australia: *Acrotelsa collaris*; *Ctenolepisma lineata*; *Ct. longicaudata* (including *Ct. urbana*); a closely allied, indeterminate species (Irish 1987); *Lepisma saccharina*; and *Lepismodes inquilinus*. Watson and Li (1967) keyed these domestic silverfish. The commonest are *Ct. longicaudata* and its close ally, grey or silver species up to 15 mm long, the former having 2–5 and the latter 9–12 sensilla on the labial palp.

Special Features of the Australian Fauna

As with the Archaeognatha, the Australian fauna is poorly known. Major factors contributing to this include the fragility of silverfish and their extreme speed when disturbed, which make the collection and preservation of intact specimens very difficult.

The four introduced genera, and the pest species belonging to them, are cosmopolitan or nearly so. *Heterolepisma* and *Acrotelsella* have wide distributions including Africa, Asia, South America and some Indian Ocean and Pacific islands (Paclt 1967). *Allatelura* is endemic, whereas *Atopatelura* and *Gastrotheus* are known from Africa, Australia and South America, and *Atelurodes* is Asian and Australian (Paclt 1963). *Trinemura* is restricted to Australia and Pacific islands (G. B. Smith 1988).

CLASSIFICATION

Order THYSANURA (28 described Australian spp.)

- | | | |
|----|------------------|------|
| | Lepidothrichidae | (0) |
| 1. | Nicoletiidae | (12) |
| 2. | Lepismatidae | (16) |
| | Maindroniidae | (0) |

The classification adopted is basically that of Remington (1954) and Paclt (1963, 1967), in which the short-bodied, inquiline Atelurinae are placed in the same family as the elongate, free-living Nicoletiinae. The Lepidothrichidae are the most primitive extant dicondy-

lous insects known, and closest to the origin of the winged insects (Wygodzinsky 1961); the other families are more specialised. The lepidothrichids and maindroniids are small families of restricted distribution.

Key to the Families and Subfamilies of Thysanura Known in Australia

1. Eyes present; body with scales, generally pigmented **Lepismatidae**
- Eyes absent; body with or without scales, white or golden **Nicoletiidae**. 2
2. Body short, oval; scales always present; appendix dorsalis and cerci short, generally much less than half body length, appendix dorsalis sometimes longer than cerci; inquiline species **ATELURINAE**
- Body subcylindrical, elongate, parallel-sided; scales generally absent; appendix dorsalis and cerci subequal, exceeding half the body length; not inquiline species **NICOLETIINAE**

1. Nicoletiidae (Figs 15.2A, D). All described Australian NICOLETIINAE belong in *Trinemura* (G. B. Smith 1988). *T. novaehollandiae* is recorded from under stones and in caves in W.A., *T. excelsa* (Fig. 15.2D) from under stones and logs in S.A., and *T. norfolkensis* from leaf litter on Norfolk I. *T. russendenensis* and *T. anemone* have been found only in caves, in Qld and N.S.W. respectively. Other nicoletiines, as yet undetermined, are known from Kangaroo I., Qld and the N.T. Mature males of *Trinemura* often have enlarged pedicels, with projecting processes. Males of *T. anemone*, *T. norfolkensis* and an undescribed species from the N.T. have unusual, anemone-like processes on the inner, proximal surface of each cercus.

Six genera of ATELURINAE (7 described species, several undescribed) are recorded from Australia. All species are small, up to 3–7 mm long. *Allatelura hilli* is associated with *Mastotermes darwiniensis* in northern Australia and, perhaps, with *Coptotermes acinaciformis* in the N.T. *Gastrotheus disjunctus* has been collected with termites in S.A. and W.A., but undetermined *Gastrotheus* have been collected with ants or termites. Species of *Atopatelura* (Fig. 15.2A) seem to predominate in southern areas, including Tas., and occur in both ant and termite nests. The host of *Atelurodes similatus* is unknown, although an

undetermined *Atelurodes* lives with the ant *Myrmecia brevinoda*. An undescribed genus and species occurs with *Coptotermes brunneus* in W.A., and another undescribed genus occurs with *Schedorhinotermes actuosus* and *Amitermes viosus* in Qld.

2. Lepismatidae (Figs 15.2B, C). The most commonly encountered group of silverfish, occurring throughout most of Australia and offshore islands, including Lord Howe. Six of the species are cosmopolitan household pests, *Ctenolepisma* predominating. Most other species are found under bark or rocks, in ant or termite nests, or in litter.

There are 5 described Australian species of *Heterolepisma* [although Paclt (1967) placed *H. hartmeyeri* in a monotypic genus *Anisolepisma*] and 5 of *Acrotelsella* (Figs 15.2B, C), plus several undescribed species of both. *H. michaelsoni* has been collected from ant nests. Undetermined *Ctenolepisma* are known from termite nests and logs in Qld, N.S.W., S.A. and W.A., and 3 undescribed species of *Lepisma* have been found in termite nests and rotting logs in northern and central Australia; both subgenera of *Lepisma*, i.e. *Lepisma* and *Tricholepisma*, are represented. At least 2 undescribed genera are present, one from litter in the Victorian mallee and one from central Australia.

Ephemeroptera

(Mayflies)

W. L. PETERS and I. C. CAMPBELL

Palaeoptera with mouth-parts mandibulate in the nymph, but vestigial and nonfunctional in the adult; abdomen of both nymph and adult with 2 or 3 long caudal filaments (cerci and terminal filament). Nymph with abdominal gills; adult with subimaginal and imaginal winged stages.

This is the most primitive order of living, winged insects and, though small, it is nearly cosmopolitan. Nymphs (Figs 16.11–14A) of all species are aquatic and occur in relatively unpolluted, standing and running freshwaters. The adults (both subimagos and imagos) (Fig. 16.1) are short lived (a few minutes to several days) and usually do not move far from water. Adults take no food and the alimentary canal of the male is inflated with air. Imagos of most species have a characteristic, aerial mating flight either over water or over nearby landmarks. A few species reproduce parthenogenetically.

Anatomy of Adult

Head (Fig. 16.1B). Usually appears triangular when viewed dorsally, with well developed posterolateral eyes. Eyes of female more or less rounded and widely separated dorsally. Eyes of male usually large, often meeting dorsally and usually divided transversely into an upper part with large facets and a lower part with smaller and usually darker facets. Males of baetids and some leptophlebiids have eyes divided into a lower rounded portion and a stalked upper portion. The exceptional development of the male eye is correlated with mating behaviour. Three ocelli present, the laterals often large. Antennae shorter to longer than head; flagellum filiform and sometimes multisegmented; scape and pedicel shorter and thicker. Mouth-parts vestigial, asymmetrical, lacking

sclerotisation and shrunk closely together in a single, externally visible, pale mass beneath the clypeus.

Thorax. Highly developed for flight. Prothorax reduced, notum shield-like. Meso- and metathorax fused together and large. Mesothorax greatly developed, its notum longitudinally grooved and strongly convex dorsally. Metathorax quadrangular and transversely ridged, sometimes produced posteriorly. Spiracles on meso- and metathorax.

Legs. Tarsi with 4 or 5 segments (rarely fewer), basal segment sometimes fused in varying degrees to tibia (Figs 16.9C, D). Pretarsal claws (Figs 16.9A, B) usually paired, both sharply hooked, or 1 hooked and 1 blunt, or both blunt. Fore legs of most males elongate (Fig. 16.1A), often as long as body, used for seizing female during mating flight. In several families the mid and hind legs of the male and all legs of the female are poorly sclerotised and probably non-functional and in the extralimital *Campsurus* (Polymitarcyidae) they appear broken off distal to the trochanter. In the North American *Dolania* (Behningiidae), the distal segments of the mid and hind legs of males break during the subimaginal moult and remain in the cast exuviae.

Wings (Figs 16.1A, 6–8). Somewhat triangular, both pairs held rigidly upright when at rest. Hind wings smaller than fore wings and with reduced venation; hind wings greatly reduced in size or absent as in Caenidae, Baetidae,

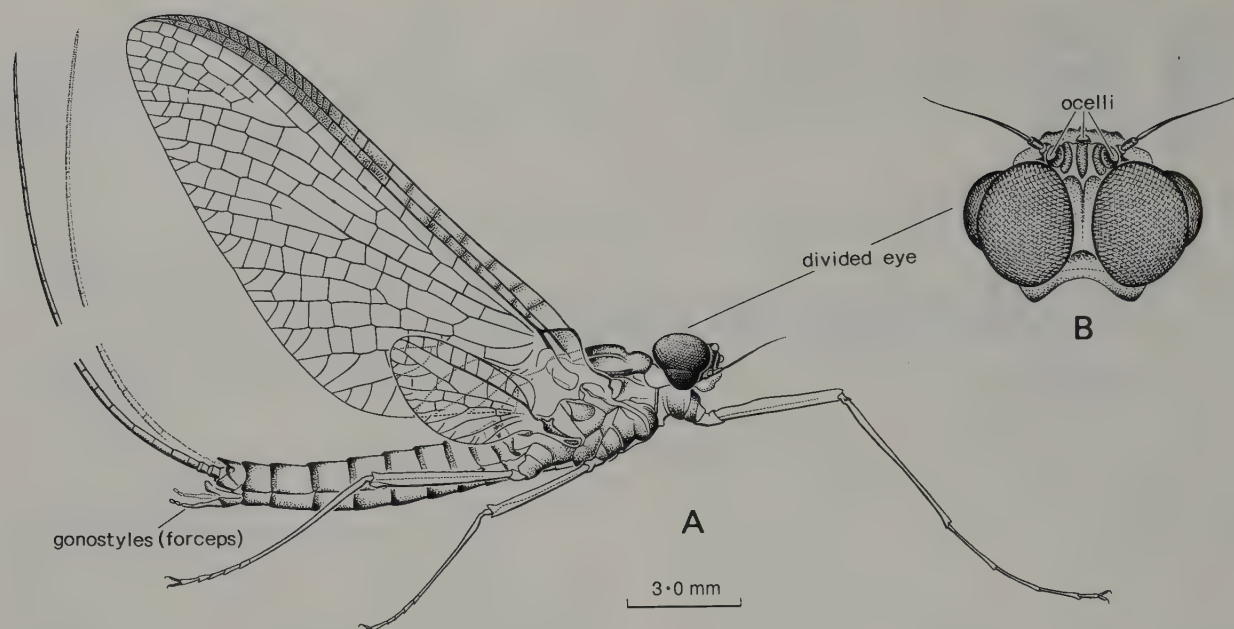


Fig. 16.1 *Atalophlebia* sp., ♂, Leptophlebiidae: A, lateral view; B, head, dorsal.

[T. Binder]

some Leptophlebiidae and the extralimital Tricorythidae. Venational nomenclature used in this chapter is as proposed by Tillyard (1932) and discussed by Edmunds and Traver (1954). Venation of fore wings sometimes reduced, e.g. in Caenidae. Wing surfaces fluted with regular alternation of convex and concave veins. In subimagos, wing membranes translucent to opaque, usually with uniform colour, sometimes with colour patterns. In imagos, membranes hyaline or translucent, sometimes with colour patterns, especially along costal margin. Anterior margin of each hind wing convex, variable, sometimes with a well developed costal projection used to couple hind wing to fore wing during flight. In *Mirawara* the veins of the posterior edge of each fore wing and the corresponding costal veinlets of the hind wing are weaker just before the margin, allowing the edge of the fore wing to roll downwards and forwards and couple with the upwardly rolled edge of the hind wing.

Abdomen. Ten-segmented, segment 1 broadly joined to metathorax. Segments 1–9 ring-like, with tergum and sternum; some species with posterolateral spines on some segments, spines occasionally pronounced. Apex of abdomen with multisegmented caudal filaments consisting of 2 lateral cerci and median, terminal filament; terminal filament sometimes reduced or absent; length of caudal filaments variable, but mostly 2 to 3 times as long as body. Spiracles on segments 1–8.

Male genitalia well developed externally (Figs 1.25D, 16.2B, D). Posterior portion of S9 enlarged into subgenital plate (styliiger plate), enlargement and shape variable. Posterior margin of subgenital plate with paired, lateral forceps (gonostyles); length and shape of forceps variable, usually basal segment long with 2 or more small apical segments, Caenidae with only 1 segment. Paired penes located dorsomedially to subgenital plate; penes

often partially to completely fused, length and shape variable, membranous and extrudable in Baetidae and Oligoneuriinae; each penis with various lobes, spines and processes.

Posterior portion of S9 of female enlarged into subanal plate, enlargement and shape variable (Figs 16.2A, C). Oviducts opening by a pair of gonopores or joined at unpaired vestibulum with common opening between S7 and S8. Duct openings of the European *Caenis robusta* are non-functional and oviposition occurs by rupture of intersegmental membranes between S7 and S8. Posterior margin of S7 (sometimes also anterior margin of S8) prolonged into a genital extension and forming a long egg guide in some Leptophlebiidae; this structure may break the surface tension of the water during egg laying.

Internal Anatomy. Alimentary tract modified for aerostatic purposes, no digestive function. Musculature well developed in thoracic cavity and male genital area. Central nervous system consists of brain, suboesophageal ganglion and usually 3 thoracic ganglia with 7 or 8 distinct abdominal ganglia. Male reproductive system with paired testes (testicular follicles numerous), each joined to separate vas deferens, seminal vesicles and separate ejaculatory ducts. Female reproductive system with numerous panoistic ovarioles joined to paired oviducts, no accessory glands.

Immature Stages

Egg (Fig. 16.4). Small (average length 0.22 mm, 0.82–0.94 mm in the Holarctic Behningiidae), of varied shape, chorionic sculpturing and colour; with 1 to several micropyles and suprachorionic sperm guides; many species with various types of attachment structures and polar cap, suprachorionic layer often adhesive.

Nymph. Morphologically different from adult, particu-

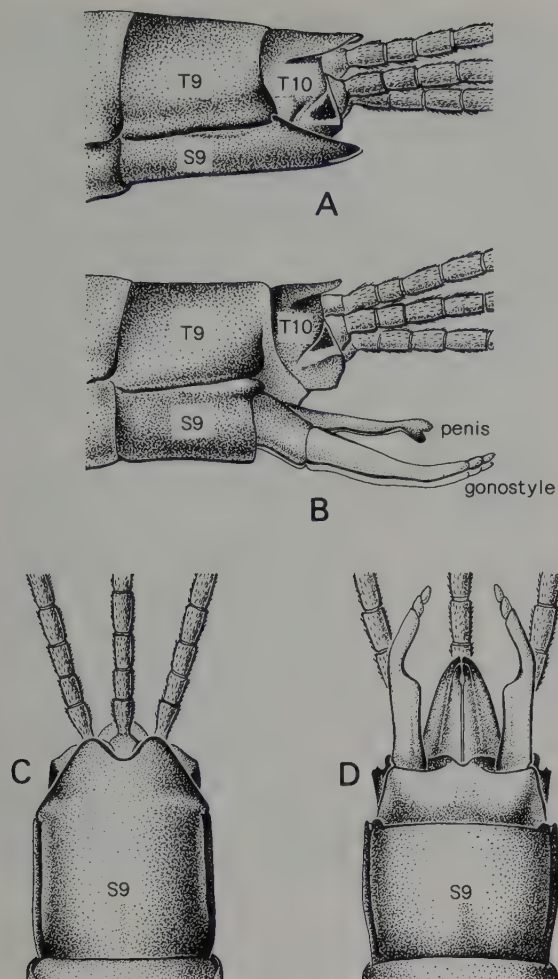


Fig. 16.2 Terminalia of *Atalophlebia* sp., Leptophlebiidae: A, ♀, lateral; B, ♂, lateral; C, ♀, ventral; D, ♂, ventral. [R. Ewins]

larly in having fully developed mouth-parts and abdominal gills (except the South American *Murphyella*); body form variable (Figs 16.11–14A).

Head (Figs 16.3A, B, 10) hypognathous to prognathous with head capsule well developed; sometimes with processes and projections. Eyes large, sexually dimorphic. Three ocelli present. Antennae shorter to longer than head; flagellum filiform and multisegmented; scape and pedicel shorter and thicker. Mouth-parts mandibulate. Labrum and clypeus well developed (Fig. 16.3D); labrum sometimes wider than head. Hypopharynx with well developed lingua (Fig. 16.3E); superlinguae well developed to absent. Mandibles with 3 condyles (Fig. 16.3C); apex of each with inner and outer incisors (usually), prostheca (usually), and molar lobe (usually), molar lobes of left and right mandibles asymmetrical so that surfaces mesh. Distal portion of each maxilla fused into galealacinia (Fig. 16.3F) bearing various hairs and spines; palps 1–multisegmented, sometimes reduced or absent; maxillae usually with distinct stipes and cardo; gills present at base of each maxilla in Oligoneuriidae, Coloburiscidae, some Baetidae and *Ameletoides*, and the extralimital

Isonychia, *Metamonius*, *Nesameletus* and *Rallidens*. Labium with small mentum and larger submentum (Fig. 16.3G), submentum sometimes greatly enlarged; glossae and paraglossae well developed, palps 2–multisegmented; paired gills present on venter of mentum near base of palps in *Coloburiscoides* and *Murphyella*. Mouth-parts highly modified in predacious species.

Thorax with 3 distinct segments, fore and hind wing pads developing on meso- and metanotum; sometimes a variety of projections on 1 to all 3 thoracic nota, well developed ridges or spines on thoracic sterna in a few genera, and thoracic sternal gills present in *Murphyella*. In *Prosopistoma* and the North American *Baetisca*, the mesonotum forms a shield-like carapace extending to abdominal segment 6 or 7 (Fig. 16.14A).

Legs shorter and stouter than in adult, hind legs usually longer than fore legs; femora more or less flattened; tarsi usually unsegmented; claw single, rarely absent, usually with denticles, shape and length of claw and denticles variable; legs with a variety of spines, tubercles and/or setae; gills present at or near base of coxae in *Isonychia*, *Murphyella* and some Baetidae; legs of some genera modified for burrowing, filtering food, grooming or gill protection.

Abdomen 10-segmented, S1 broadly fused to metathorax; terga sometimes with paired or unpaired spines and/or tubercles; posterolateral tergal spines usually present, spines often small but sometimes greatly expanded.

Abdominal gills (Figs 16.14B, C, 15) present on abdominal segments 1–7 (rarely 8), or absent from 1 or more segments in various combinations; gill position variable, either ventral, lateral or dorsal; gill structure highly variable, the first gill pair often dissimilar to remaining gill pairs. Abdominal gills absent in *Murphyella*.

Apex of abdomen with multisegmented caudal filaments consisting of 2 lateral cerci and a terminal filament; terminal filament sometimes reduced or absent; length of caudal filaments varies from shorter than to several times longer than body; caudal filaments with various (sometimes dense) setae, spines and denticles. The caudal filaments of *Prosopistoma* can be retracted into the abdomen.

Biology

Imagos. Most imagos live no more than 24 hours. Some live only a few minutes while others, especially in colder climates, live for several days. Reproduction and dispersal are the sole functions of mayfly imagos. Adults usually do not move far from water, but some species may be found several kilometres from their emergence site. Mated females of some species of Holarctic burrowing mayflies are known to make long upstream flights before oviposition.

Imagos usually swarm, mate and oviposit at a specific time of the day. The time of swarming is characteristic for a species and is influenced by cloud cover, light intensity, temperature and other weather factors. In temperate areas imagos generally swarm during the warmer period of midday to dark while species living in more tropical areas

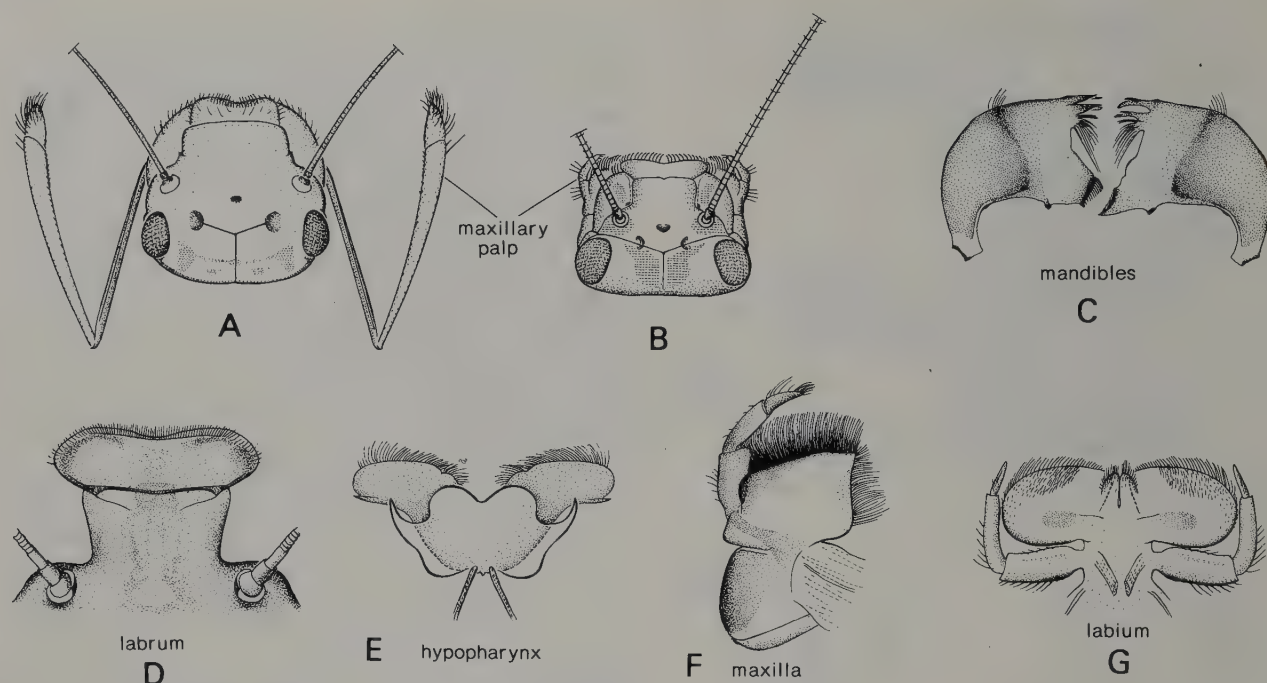


Fig. 16.3 Nymphs of Leptophlebiidae: A, *Atalophlebia yugana*, head, dorsal; B–G, *Atalophlebioides* sp., head and mouth-parts.

[A by J. Peters; B–G by M. Quick, R. Ewins]

may swarm from before dawn to mid-morning. In genera such as *Prosopistoma* where the adult is very short-lived or the female is mature as a subimago, factors determining emergence of subimagos necessarily are those which also determine swarming.

Swarms of mayflies characteristically consist of several to many thousands of males flying in an up and down pattern over water or nearby land objects. When the companies of males are small, swarming occurs over a specific swarm marker, such as a rock, bush, tree, light-coloured object, bridge or shore line. The type of marker and whether the swarm is found over land or water are different for each species (Savolainen 1978). Large swarms of some burrowing mayflies may cover an entire body of water. When imaginal emergence is synchronised over a short period, swarms are much larger than when emergence extends over many months.

In a few species males fly in a horizontal pattern as they search for females. According to Riek (1970), males of some Caenidae and *Atalophlebia* patrol stretches of streams. Swarming is usually a male activity with females entering the swarm, but males and females of Caenidae and Tricorythidae both participate in such flights.

Reproduction. Copulation (Fig. 1.26) normally takes place in flight. For the Holarctic *Parametetus* the male generally approaches the female from below, his long fore legs extend upward and his tarsi curve around the female wing bases while his abdomen recurves up and back so the genital forceps grasp the apex of the female abdomen (the female curves her abdomen so the penes can be inserted easily into the opening of her S7) (Brinck 1957). However, the external genitalia of some mayflies are highly modified and the details of copulation vary.

Mating may last from a few seconds to several minutes, but usually less than a minute.

Mayfly eggs are deposited in water. Most females oviposit by descending to the water, dipping the abdomen into the water and releasing a few eggs at a time; such behaviour is displayed by many Australian Leptophlebiidae. Some species, such as *Coloburiscoides haleuticus*, release all their eggs in a single batch that separates immediately on contact with water. In other species, the female enters the water for oviposition, either placing the apex of the abdomen below the surface (some Australian species of *Atalophlebia*) (Riek 1970) or crawling beneath the surface to deposit eggs on stones or other substrates on the bottom (some Northern Hemisphere species of *Baetis*). Oviposition by Caenidae is effected by rupture of the abdominal wall upon contact with water (Soldán, pers. comm.).

Fecundity varies from about 100 eggs in *Prosopistoma* and Behningiidae to 12 000 eggs in the extralimital *Palingenia*; however, most species range from 500 to 3000 eggs. Parthenogenesis is known for about 50 species, although obligatory in only a few. Some species of *Cloeon* and the extralimital *Callibaetis* are ovoviparous; female imagos oviposit up to 3 weeks after mating and as soon as the eggs contact the water young nymphs hatch.

Immature Stages. The period of egg development varies from a week to a year, depending on species and temperature. For some European species without diapause, egg development takes 2–3 weeks at optimum temperatures, but much longer at colder temperatures (Humpesch 1984). Australian species have a wide range of developmental times (Campbell 1986). Winter dia-

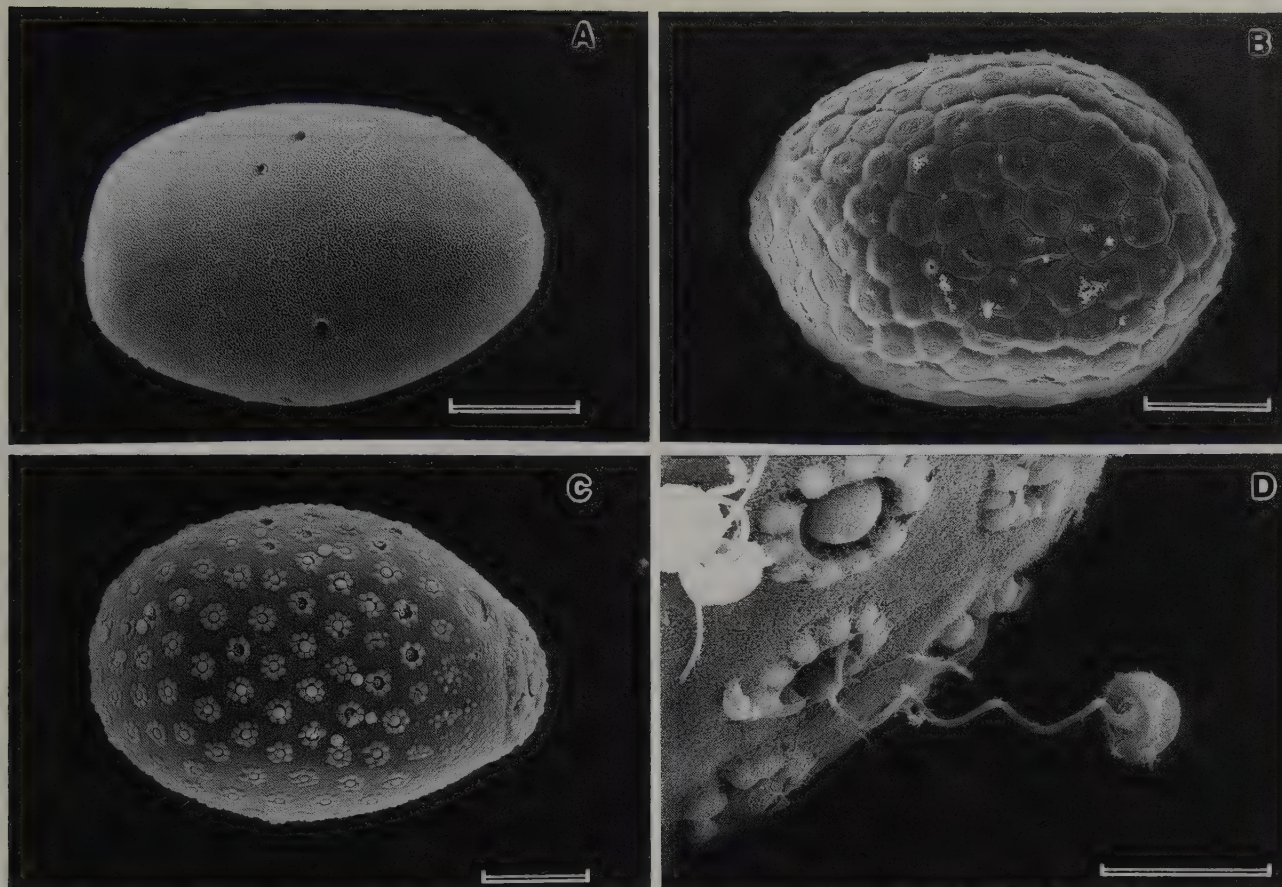


Fig. 16.4 Eggs: A, *Tasmanophlebia lacuscoerulei*, Oniscigastridae; B, *Kirrara procera*, Leptophlebiidae; C, D, *Coloburiscoides haleuticus*, Coloburiscidae, with detail of adhesive structure. Scales: A–C = 50 μ m; D = 10 μ m.

pause, which is known for a few Holarctic species, appears to occur in *Coloburiscoides giganteus* and *Baetis soror* in Australia. Summer egg diapause is also likely for several species including *Atalophlebia australasica* which occurs in temporary streams. Eggs of some species demonstrate asynchronous development, or delayed hatching, which possibly involves diapause (Hynes 1970). *Kirrara procera* has a short oviposition period but young nymphs are found every month (Campbell and Holt 1984). Eggs developing parthenogenetically develop more slowly than fertilised eggs.

The duration of nymphal development varies from 3 weeks in the North American *Parameletus columbiae* to 3 years in some temperate, burrowing mayflies. Mayflies have 10–50 nymphal instars depending on species, diet and temperature, but 15–30 is most common. Diet and water temperature determine rate of growth, and light appears to play only an indirect role (as it affects water temperature and algal growth). Life cycles are either uni-, bi- or multivoltine, depending on species. In the tropics, non-seasonal, multivoltine cycles predominate, and towards the Arctic, seasonal, univoltine cycles (Brittain 1982). In New Zealand (Towns 1981, 1983a) and Australia (Riek 1970; Campbell 1986), most species are univoltine but life cycles range from 6 months to 3 years. Many Australian species have overlapping broods and

unsynchronised development, and their life cycles are less seasonal than is the case in univoltine species of the Northern Hemisphere. A few, such as *Kirrara procera*, do show a seasonal, univoltine pattern with a single cohort of nymphs (Campbell and Holt 1984).

In Swedish ponds, *Cloeon inscriptum* overwinters without oxygen under ice in an anaerobic diapause induced by decreasing water temperatures (Nagell 1980). Nymphal diapause, frequently suggested, is as yet unconfirmed for other species. Temperature limits for growth may vary by species, population or developmental stage, and cold winters or hot dry summers may induce strong seasonal patterns without a true diapause.

Nymphs of each species are normally restricted to a particular type of habitat, ranging from lakes and large rivers to temporary ponds and streams. A very few species occur in stagnant, lowland, weed-choked backwaters and bogs, while many occur on stones and rocks (i.e. are *epilithic*) in high, cold, snow-melt streams. In Australia, the mayflies inhabiting lowland, standing or slowly flowing waters include the small, swimming nymphs of *Cloeon*, the large, flattened, clinging nymphs of the *Atalophlebia australasica* group of species, and *Tasmanocoenis*. Swimming nymphs often have enlarged, overlapping rows of hairs on the inner surfaces of the cerci and lateral surfaces of the terminal filament, these

together forming a paddle. In one species from New Caledonia the swimming paddles are formed by enlarged femora. Nymphs of *Prosopistoma* resemble small, well-camouflaged crustaceans and are found underneath large rocks in the fastest parts of rivers or small streams.

The sprawling nymphs of *Austrophlebioides* are the most commonly encountered mayflies in upland Australian streams. They occur on surfaces of stones in moderate currents. In areas of rapid current, nymphs of *Kirrara*, with greatly enlarged abdominal gills forming an adhesion disc, occur on the tops of stones and *Coloburiscoides*, with gills modified to provide anchorage, occur beneath stones. *Neboissophlebia* nymphs are also abundant in these streams, where they are often associated with accumulations of leaves.

Tasmanophlebia and several species of *Atalophlebia* may be found on stones in upland lakes. The streamlined nymphs of *Ameletoides* also occur in lakes of the Snowy Mountains, but not in Tasmanian lakes, although they are characteristic of small, cool, upland streams in both regions.

Burrowing mayflies (superfamily Ephemeroidea) in other countries are morphologically remarkable with the legs, frontal processes of the head and mandibular tusks all modified; feathery gills well-supplied with tracheae constantly pump water through the burrow. Wood-boring, South American *Asthenopus* (Polymitarcyidae) line burrows with wood chips and secretions from the Malpighian tubules. Some non-Ephemeroidea in Australia show degrees of burrowing behaviour. Nymphs of *Jappa* burrow under stones in silty sections of sluggish streams, and have long setae on the gill margins. *Tasmanophlebia* and *Tasmanocoenis* settle into sand or silt until they are almost completely hidden; in both genera, the anterior gill is modified into a protective cover for the remaining gills.

Legs and mouth-parts are also modified for feeding. Most mayflies scrape or graze detritus, diatoms and algae from rocks and leaves. Some, such as *Coloburiscoides*, are filter feeders and a few, such as *Mirawara*, are carnivores. Feeding ceases some time during the last nymphal instars as the digestive system degenerates and adult structures complete development. Nymphs often move to another habitat during this period, frequently toward the sides of rivers where they will eventually emerge.

Subimago. Mayflies emerge as winged subimagos, which usually moult to imagos, or true adults (Edmunds and McCafferty 1988). They are the only insects that undergo an ecdysis after having acquired functional wings. Some nymphs emerge to subimagos in a few seconds on the surface film of water, while others crawl out on rocks and sticks and emerge slowly, taking up to five minutes. Emergence appears to require a minimum water temperature and some seasonal cue such as a temperature change or a full moon, emergence occurring several hours to days after a particular cue. Different species emerge at different times during the diel cycle. *Tasmanocoenis* normally emerge shortly after dawn whereas those leptophlebiids that emerge on the surface film of lakes prefer the warmer midday. The nymphs of *Ameletoides* and *Tasmanophlebia* crawl out of the water onto rocks at

dusk to emerge. Subimagos of some species cling to rocks overnight and are ready to fly with the first light, while others fly away immediately after emergence.

Subimagos usually rest with little movement in bushes and trees and for most species the stage lasts about 24 hours. Cooler temperatures can extend the subimaginal stage up to several days. Some Caenidae moult to imagos in five minutes or less. In *Tasmanocoenis*, moulting usually takes from 10–20 seconds, measured from the time the subimagos alight on an object to the time the imagos fly off to join the swarm; imagos often take flight before the caudal filaments are free of the subimaginal exuvia.

In *Prosopistoma*, in the Papuan *Plethogenesia* and other Palingeniidae, and in some Northern Hemisphere families, the female subimagos mate and die without moulting.

Subimagos (and imagos) may be strictly seasonal or present nearly all year. The latter pattern is common in warm, tropical areas, while in colder, temperate areas subimaginal emergence tends to occur during the warmest periods. However, non-seasonal life cycles predominate in New Zealand (Towns 1981, 1983a) where the potential emergence period is long and the entire mayfly fauna in New Caledonia (all Leptophlebiidae) is highly seasonal (Peters unpubl.). In Australia, the subimaginal emergence of mayflies is not strongly seasonal (Campbell and Holt 1984, 1986). One species of *Austrophlebioides* emerges over 4–5 months during the summer (Duncan 1972) and *Koorrnonga inconspicua* emerges over 10 months during autumn-spring (Suter 1980). *Tasmanocoenis tillyardi* emerges over 6 months during spring-autumn with two distinct generations (Suter and Bishop 1980).

Natural Enemies. Mayfly nymphs and adults are important food items for many freshwater fish. Nymphs may be eaten on the stream bottom, as they drift in the current or swim to the surface, or on the surface as they emerge to the subimago. Many nymphs are also eaten by the carnivorous nymphs and larvae of other aquatic insects (Odonata, Plecoptera, Coleoptera and some Ephemeroptera). Adults are ensnared in spider webs spun over or beside streams and others are eaten by insectivorous birds and Odonata. Emerging mayflies are food for streamside amphibians, mammals and man. Szent-Ivany and Ujházy (1973) described cakes made of adult mayflies (probably the large burrower *Plethogenesia*) by natives of the Sepik River region in Papua New Guinea.

Fungi (Trichomycetes), algae, Protozoa (Peritrichidae), some tube-dwelling Chironomidae and some Simuliidae (DIPT) are phoretic commensals on nymphs; but *Symbiocladius* (Fig. 16.5) is ectoparasitic (Riek 1970, 1974a; Hynes 1976a; Arvy and Peters 1976). Nymphs are intermediate hosts for certain Trematoda which parasitise fish, and both nymphs and adults are sometimes parasitised by Nematoda.

Economic Significance. Mayflies are important in the trophic structure of aquatic environments. Nymphs are mostly collector-gatherers or scrapers although some are predator-engulfers (Merritt and Cummins 1984; Edmunds 1984). Nymphs and adults, in turn, are preyed on by

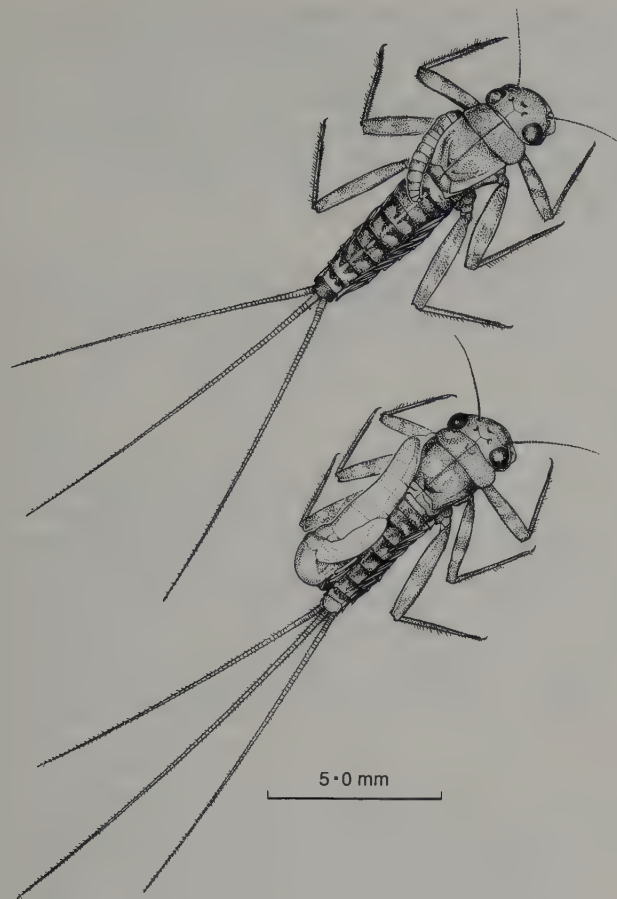


Fig. 16.5 Parasitic larva and pupa of *Symbiocladius* sp., Chironomidae, on nymphs of *Austrophlebioides* sp., Leptophlebiidae. Young larvae face in the same direction as the nymph, but older larvae and pupae always face posteriorly. [S. Monteith]

many aquatic predators, including sport fish. The particular species, overall diversity and abundance of mayflies can indicate water quality. Mayflies help to purify freshwaters; filter feeders especially remove large amounts of particulate nutrients. Adults of a few species may swarm to lights and become a nuisance in towns near lakes, and great swarms may provoke allergies in sensitised individuals. Nymphs of Asthenopodinae, such as the South-East Asian *Povilla corporaali*, excavate wood and wooden structures in water, including boats and irrigation gates (Vejabhongse 1937).

Special Features of the Australian Fauna

Australia has representatives of nine of the 23 extant mayfly families. Of the superfamilies, only the Ephemeroidea are not represented. The mayfly faunas of Australia, New Zealand and temperate South America are strikingly similar. This is evident in the Leptophlebiidae, Siphonuridae, Oniscigastridae, Ameletopsidae and Coloburiscidae, and the presence of these families in Australia is the result of Gondwanan dispersals. Certain elements of the Australian mayfly fauna are northern in origin, e.g. the Ephemerellidae, a few Leptophlebiidae, Prosopistomatidae, Caenidae and probably most Baetidae. Ephemeridae are known from New Zealand and Palingeniidae from New Guinea. Heptageniidae, Tricorythidae and Neoephemeridae are widespread through the Sunda Is.

Mayflies are most abundant in the highlands of south-eastern Australia and in Tas., but there are numerous species in the colder sections of east coast streams as far north as Cape York Peninsula. There are several species in the wet south-western corner of W.A. and a few, widely distributed species in the slow-flowing, inland streams of the eastern states.

CLASSIFICATION

Order EPHEMEROPTERA (84 Australian spp.)

Suborder SCHISTONOTA (77)

BAETOIDEA (20)

1. Siphonuridae (1)
2. Baetidae (13)
3. Oniscigastridae (3)
4. Ameletopsidae (3)
- Ametropodidae (0)

HEPTAGENIOIDEA (3)

5. Coloburiscidae (3)
- Oligoneuriidae (0)
- Isonychiidae (0)
- Heptageniidae (0)

LEPTOPHLEBIOIDEA (54)

6. Leptophlebiidae (54)

Suborder PANNOTA (7)

EPHEMERELLOIDEA (1)

7. Ephemerellidae (1)
- Leptohyphidae (0)
- Tricorythidae (0)

CAENOIDEA (6)

- Neoephemeridae (0)
- Baetiscidae (0)

EPHEMEROIDEA (0)

- Behningiidae (0)
- Potamanthidae (0)
- Euthyplociidae (0)
- Polymitarciidae (0)
- Ephemeridae (0)
- Palingeniidae (0)
8. Caenidae (5)
9. Prosopistomatidae (1)

There has been little agreement concerning the classification of this order (Ulmer 1920; Handlirsch 1922; Needham *et al.* 1935; Burks 1953; Edmunds and Traver 1954; Demoulin 1958; Edmunds 1962; Landa 1969; Chernova 1970; Riek 1973d; McCafferty and Edmunds 1979; Landa and Soldán 1985). The classification used

here and in Campbell (1988) is that of Landa and Soldán (1985), except that the Coloburiscinae of the Oligoneuriidae are treated as a separate family—Coloburiscidae. Further, the fossil taxa and extant subfamilies given in Landa and Soldán (1985) are not included here.

The suborders and superfamilies are evolutionary con-

cepts which have never been defined morphologically in both nymphs and adults and present definitions of the families Siphonuridae, Oniscigastridae, Ameletopsidae and Coloburiscidae are based on nymphs only. The classification of Landa and Soldán (1985) is based upon comparative internal anatomy. In the keys below, we use

external morphological characters of the Australian representatives of the families rather than the family characteristics given by Landa and Soldán.

The Heptageniidae were mistakenly recorded in the Australian fauna by Harker (1950, 1954). Campbell (1988) has catalogued the Australian species.

Keys to the Families of Ephemeroptera Known in Australia

ADULTS

1. Vein MA₂ of fore wings entirely detached basally from stem of vein MA (Fig. 16.7A), or vein MA apparently unforked (Fig. 16.8A) 2
 Vein MA of fore wings forked (Figs 16.6A–D, 7B, D, 8B, C) or vein MA₂ attached at base to vein MA₁ by a cross-vein (Fig. 16.7C) 3
- 2(1). Short, basally detached, single or double, marginal intercalaries present in centre of each interspace of fore wings (Fig. 16.7A); hind wings present or absent (if present with no more than 3 longitudinal veins) **Baetidae**
 Long, basally detached, double, marginal intercalaries present near longitudinal veins of fore wings of males (Fig. 16.8A), or intercalaries absent in fore wings of females; hind wings present (with more than 3 longitudinal veins as in Fig. 16.8A) **Prosopistomatidae**
- 3(1). Vein MA₂ of fore wings attached at base to vein MA₁ by a cross-vein (Fig. 16.7C); genital forceps of male 1-segmented; hind wings absent **Caenidae**
 Vein MA of fore wings forked (Figs 16.6A–D, 7B, D, 8B, C); genital forceps of male with 2 or more segments (Figs 16.2B, D); hind wings present 4
- 4(3). Cubital intercalaries in fore wings usually detached basally from a longitudinal vein, or 1 or more intercalaries attached to vein CuA or CuP by a cross-vein (cross-vein sometimes appears as a fork) (Figs 16.6B–D, 7D) 5
 Cubital intercalaries in fore wings consist of a series of veinlets, often forking, and attaching vein CuA to hind margin (Figs 16.6A, 7B, 8B, C) 6
- 5(4). Two short, basally detached, marginal intercalaries present in interspace between veins MP₂ and CuA of the fore wings (Fig. 16.7D); genital forceps of male with 1 short terminal segment **Ephemerellidae**
 No marginal intercalaries present in interspace between veins MP₂ and CuA of the fore wings (Figs 16.6B–D); genital forceps of male with 2 short, terminal segments, segmentation often indistinct (Figs 16.2B, D) **Leptophlebiidae**
- 6(4). Fore wing margin between veins CuA and CuP smoothly curved, tornus midway between veins CuA and CuP (Fig. 16.8B); 2 or more cubital intercalaries forked in fore wings (Fig. 16.8B); fore claw appears single (hypertrophied in male), one of the pair reduced (Fig. 16.9A) **Coloburiscidae**
 Fore wing margin between veins CuA and CuP straight to slightly curved, tornus close to vein CuA; cubital intercalaries of fore wings unforked, or sometimes with one fork (Figs 16.6A, 7B, 8C); fore claw paired (Fig. 16.9B) 7
- 7(6). Vein MP₂ of fore wings attached at base to vein CuA (Fig. 16.8C); terminal filament multisegmented, nearly equal in length to cerci **Siphonuridae**
 Vein MP₂ of fore wings attached at base to vein MP₁, directly or by cross-vein or intercalary (Figs 16.6A, 7B); terminal filament much shorter than cerci, with 1 to a few segments 8
- 8(7). First tarsal segment of hind legs (partially fused to tibia) less than half as long as tibia (Fig. 16.9C); base of vein MP₂ of fore wings attached to intercalary of vein MP, intercalary attached to vein MP₁ (Fig. 16.7B); vein MP of hind wings forked in basal half of wings **Ameletopsidae**
 First tarsal segment of hind legs (partially fused to tibia) a little shorter than tibia (Fig. 16.9D); base of vein MP₂ of fore wings attached to vein MP₁ (Fig. 16.6A); vein MP of hind wings forked in apical half of wings **Oniscigastridae**

NYMPHS

1. Mesonotum forms a shield-like carapace extending to abdominal segment 7 (Fig. 16.14A); caudal filaments retractable into abdomen **Prosopistomatidae**
 Mesonotum without a shield-like carapace (Figs 16.11–13); caudal filaments not retractable 2
- 2(1). Abdominal gills on segment 1 operculate, covering remaining gills; gills on abdominal segments 1–4 (Fig. 16.13F) **Oniscigastridae**
 Abdominal gills on segment 1 not operculate, not covering remaining gills; gills on abdominal segments 1–5, 1–6, 1–7, 2–6 or 2–7 (Figs 16.11A, B, 12A, B, 13A–E) 3
- 3(2). Abdominal gills on segment 2 operculate and quadrate (Fig. 16.12B) **Caenidae**
 Abdominal gills on segment 2 neither operculate nor quadrate, although other gills sometimes semi-operculate (Figs 16.11A, B, 12A, 13A–E) 4
- 4(3). Abdominal gills on segments 2–6 (Fig. 16.13E); ventral lamella of each gill subdivided into 2 series of small, overlapping lobes **Ephemerellidae**
 Abdominal gills on segments 1–5, 1–6, 1–7 or 2–7 (Figs 16.11A, B, 12A, 13A–D); ventral lamella of each gill plate-like (Fig. 16.15), fibrilliform (Figs 16.14B, C) or absent 5
- 5(4). Dorsal lamella of each abdominal gill sclerotised, bifid and with heavy spines (Figs 16.11B, 14B); ventral lamella unsclerotised, fibrilliform **Coloburiscidae**

- Dorsal lamella of each abdominal gill usually plate-like, neither sclerotised, bifid nor spinose (Figs 16.11A, 12A, 13A–D, 14C) ventral lamella plate-like (Fig. 16.15), fibrilliform (Fig. 16.14C) or absent 6
- 6(5). Clypeus apparently fused to frons (Figs 16.3A, B, 10B) 7
- Clypeus distinctly separated from frons by epistomal suture (Figs 16.10A, C) 8
- 7(6). Dorsal portion of each abdominal gill plate-like and ventral portion fibrilliform (Figs 16.11A, 14C); maxillary and labial palps multisegmented **Ameletopsidae**
- Gills variable, but dorsal and ventral portions similar in shape and structure (ventral portion occasionally lost) (Fig. 16.15); maxillary and labial palps 3-segmented, although segmentation often indistinct (Figs 16.3A, B, F, G) **Leptophlebiidae**
- 8(6). Antennae short, length less than length of head (Fig. 16.10C); posterolateral projections present and usually well developed on abdominal segments 8–9 **Siphonuridae**
- Antennae long, length more than twice length of head (Figs 16.10A, 12A); posterolateral projections weakly developed or absent **Baetidae**

Suborder SCHISTONOTA

Superfamily BAETOIDEA

1. Siphonuridae. The family is represented in Australia by *Ameletoides lacusalbinae*. Nymphs, with their streamlined shape and single, plate-like, abdominal gills, resemble large baetids (Fig. 16.10C); in addition to the abdominal gills nymphs have single gills on each maxilla.

A. lacusalbinae is widespread in high altitude streams in south-eastern, mainland Australia and Tas. (Tillyard 1933; Campbell 1981, 1986) and near Mt Kosciusko also occurs in lakes. Nymphs are algal scrapers (Campbell 1985) and, on the mainland at least, nymphal development ranges from less than 1 year to 2 years. Adults emerge from September to January, each female producing about 11 000 eggs.

2. Baetidae. Baetids are extremely widespread and abundant in Australia. *Baetis* (4 spp.), *Cloeon* (5 spp.), *Centroptilum* (2 spp.) and *Pseudocloeon* (1 sp.) are cosmopolitan while *Bungona* (1 sp.) is endemic. The family has received comparatively little study in Australia and undoubtedly there are undescribed species.

Nymphs are small (less than 1 cm long), slender and streamlined, with plate-like gills. They differ from nymphs of siphonurids by their smaller size and longer antennae (Fig. 16.10A), and in the structure of the labrum. Adults have transparent wings with reduced venation. *Bungona*, *Cloeon* and *Pseudocloeon* all lack hind wings.

In males the compound eyes are divided completely with the dorsal part developed into a large, turbinate structure. The eyes of females are small and comparatively simple. The penes of the male are membranous and extrudable.

Baetis occurs only in permanent, flowing water and are most common in the clear water of cold streams. The genus is widespread in Tas., the eastern mainland (including S.A.) and the south-west of W.A. (Bunn *et al.* 1986). Nymphs appear to feed mostly by scraping algae and fine particulate detritus from solid surfaces (Chessman 1986). One species of *Baetis* in a Victorian high mountain stream is univoltine with a summer emergence period (November–March) (Duncan 1972). *Baetis soror* is univoltine in one S.A. stream and bivoltine in another; both populations have multiple cohorts, with emergence over at least 9 months of the year (Suter 1980; Suter and Bishop 1980).

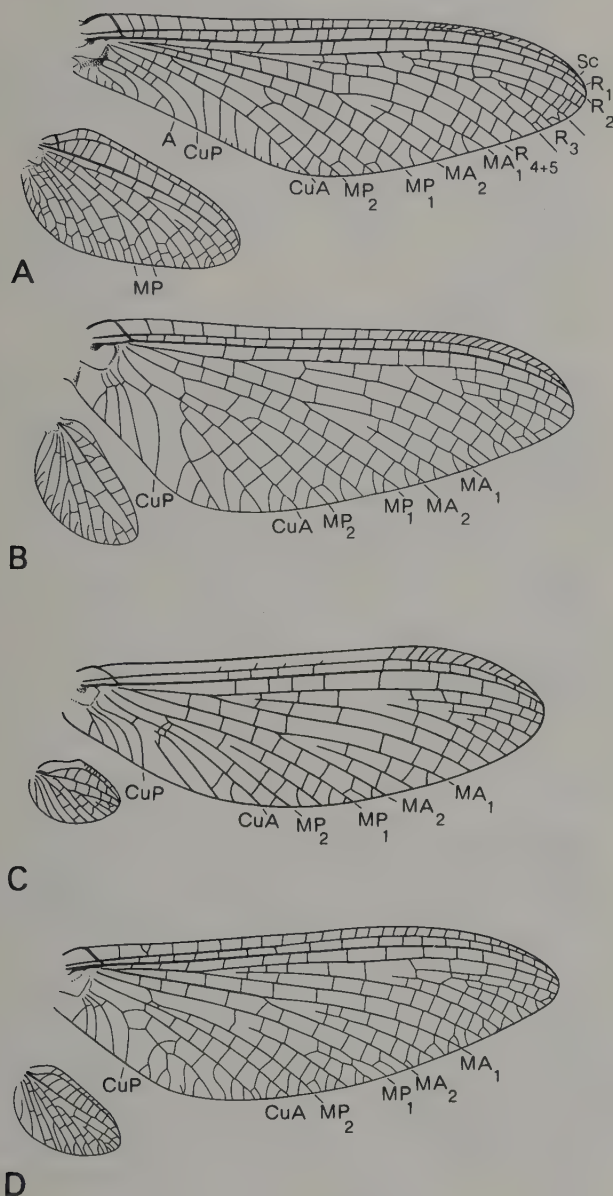


Fig. 16.6 Wing venation: A, *Tasmanophlebia* sp., Oniscigastridae; B–D, *Leptophlebiidae*: B, *Atalophlebia* sp.; C, *Nousia* sp.; D, *Jappa* sp.

[M. Quick]

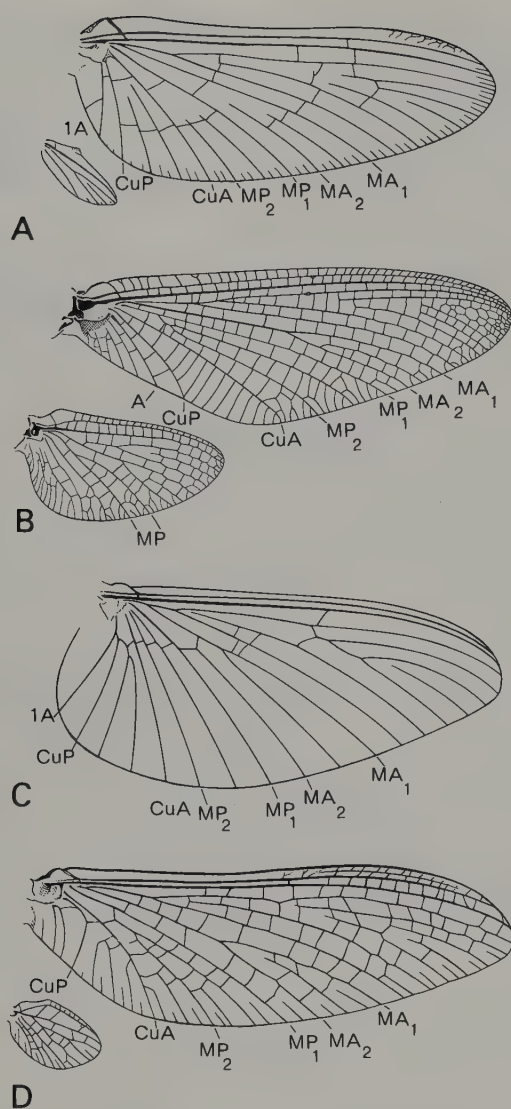


Fig. 16.7 Wing venation: A, *Baetis* sp., Baetidae; B, *Mirawara* sp., Ameletopsidae; C, *Tasmanocoenis* sp., Caenidae; D, *Ephemerellina* (*Austremerella*) sp., Ephemerellidae. [M. Quick]

Centroptilum and *Baetis* occur in similar habitats and sometimes together, but generally *Centroptilum* is absent from north-eastern Australia. Nymphs are generally larger than those of *Baetis* and have greatly elongated tarsal claws but apparently they feed in a similar fashion.

Cloeon is widespread in eastern Australia from Tas. to the tropics. Nymphs are most common in standing waters such as billabongs and farm dams and are also found in slowly flowing reaches of rivers. Nymphs of at least one species feed mostly on filamentous algae (Chessman 1986). In a seasonal creek in the N.T., nymphs of *Cloeon fluviatile* develop rapidly (about 4 weeks) and eggs can resist desiccation during dry months (Marchant 1982).

Bungona narilla was collected from a small coastal stream near Sydney but nothing more is known of its biology. *Pseudocloeon* is very small and occurs in the mountain streams of coastal Qld and N.S.W. (Riek 1970).

3. Oniscigastridae. The family is represented in

Australia by *Tasmanophlebia*. Nymphs are large with the first abdominal gills covering the other gill pairs (Fig. 16.13F). Adults have transparent wings with the wing bases washed with intense orange or dark brown.

T. lacustris is recorded from Tas., and *T. lacuscoerulei* and *T. nigrescens* from the south-eastern mainland. The genus occurs on the mainland from Barrington Tops, N.S.W., to the Fleurieu Peninsula, S.A. and is also present on Flinders I. in Bass Strait. Nymphs occur in upland lakes and the sandy, silty, slowly flowing reaches of usually small streams (where they sometimes burrow), and

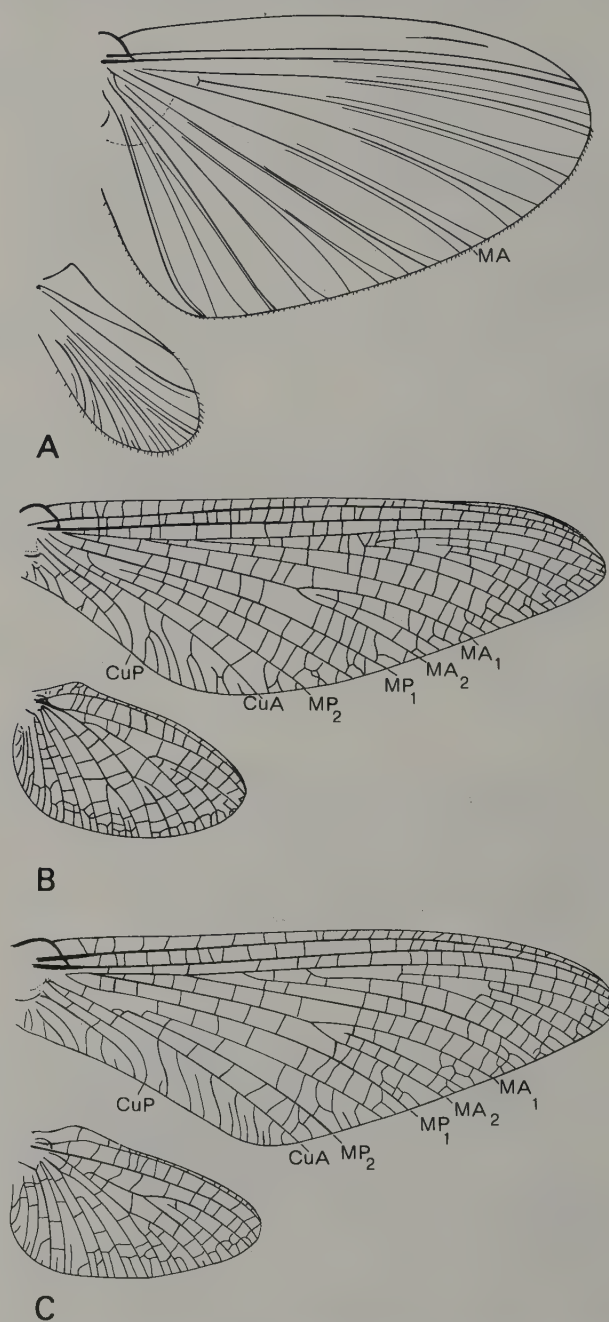


Fig. 16.8 Wing venation: A, *Prosopistoma* sp., Prosopistomatidae (drawn from Malaysian subimago); B, *Coloburiscoides* sp., Coloburiscidae; C, *Ameletoides* sp., Siphonuridae. [J. Peters]

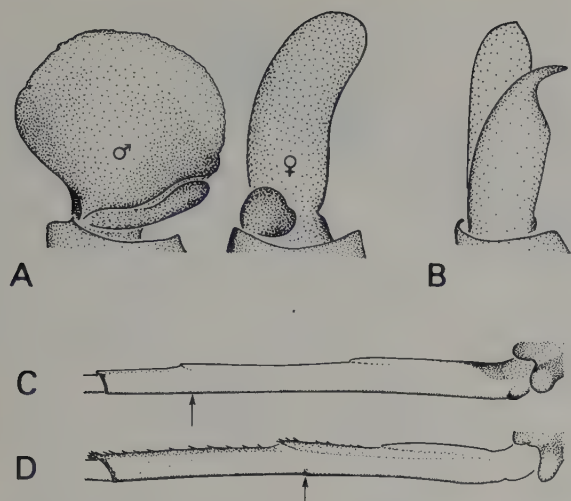


Fig. 16.9 Adults. Fore claw of: A, Coloburiscidae; B, Oniscigastridae. Fused patello-tibia and first tarsal segment of hind leg of: C, Ameletopsidae; D, Oniscigastridae; arrow indicates point of partial fusion of tibia and first tarsal segment. [J. Peters]

over altitudes from near the summit of Mt Kosciuszko (about 2000 m) to almost sea-level in small, coastal streams. Nymphs feed on fine particulate detritus (Campbell 1985).

An undescribed species of *Tasmanophlebia* in a small, sub-alpine stream was found to be basically univoltine, but with some early emerging individuals giving rise to a second summer generation (Campbell 1986). Nymphs leave the water prior to ecdysis, and emergence occurs at dusk during November–March. Each female produces about 1500 eggs. Males of *T. lacuscoerulei* have been observed swarming near the edges of a lake in the middle of a hot, summer day, while males of *T. lacustris* swarm some distance from the water. No species of *Tasmanophlebia* appear to be attracted to lights.

4. Ameletopsidae. Nymphs of *Mirawara* (3 spp.) are large with prognathous heads (Figs 16.10B, 11A) and gills bearing both a plate-like lamella and a tuft (Fig. 16.14C). Adults are unique among Australian mayflies in often having red or purple wings. The genus is widespread on the mainland from Cairns to near Melbourne (Campbell 1981).

Nymphs are nocturnal and carnivorous, feeding mainly on other mayflies and chironomids which they engulf whole (Campbell 1980, 1985). They occur in stony, upland streams where they appear to require large cobbles for shelter. The life history of *M. aapta* is quite variable, occupying 10–18 months (Campbell 1986). Nymphs undergo their final ecdysis on the stream bed and subimagos rise through the water to emerge directly from the water surface. Adults are present from October to April, and females may be seen during the day depositing eggs in small groups on the surface of river pools. Each female produces about 8000 eggs.

Superfamily HEPTAGENIOIDEA

5. Coloburiscidae. *Coloburiscoides* (5 spp.) are known from the south-eastern mainland (Lestage 1935; Riek

1955e, though Riek's redefinition of *Coloburiscoides* is incorrect and applies to the New Zealand genus *Coloburiscus*). *Coloburiscoides* nymphs have mouth-parts modified for filter feeding (Fig. 16.11B) and 2 pairs of finger-like, oral gills as well as abdominal gills. Each of the latter consists of a bifid, spinose lamella and a basal tuft of filaments (Fig. 16.14B). Both the oral gills and the tufts of the abdominal gills have large numbers of chloride cells and appear to be both osmoregulatory and respiratory (Filshie and Campbell 1984). The spinose structures of the gills appear to anchor nymphs beneath rocks in stony, upland streams.

Nymphs trap fine, particulate, organic material and algae with their mouth-parts and fore legs (Campbell 1985). Nymphal development takes from 6 months to 2 years with emergence in most species occurring directly from the water surface (Campbell 1986). The emergence period is variable ranging from 4 months (November–March) for *C. giganteus* to 9 months (August–April) for *C. haleuticus* (Campbell 1986). Adults of *C. haleuticus* and at least one other undescribed species from the Snowy Mountains swarm above streams at dusk, often using bridges as markers. Females of *C. munionga* pro-

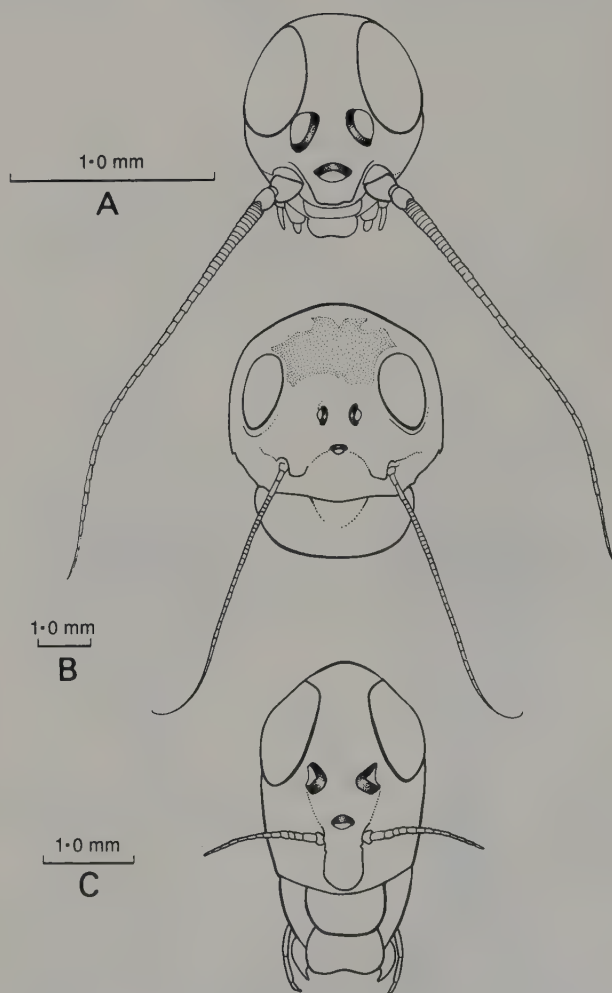


Fig. 16.10 Heads of nymphs: A, *Baetis* sp., Baetidae; B, *Mirawara* sp., Ameletopsidae; C, *Ameletoides* sp., Siphonuridae. [A. Hastings]

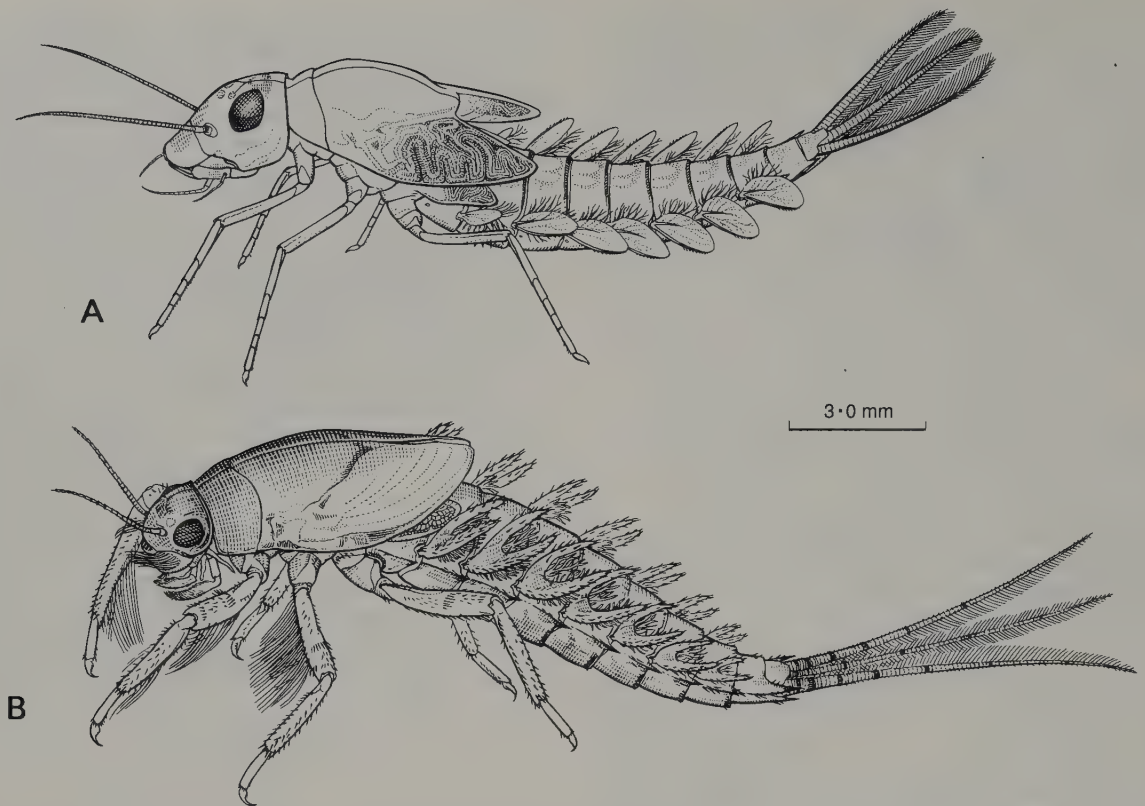


Fig. 16.11 Nymphs: A, *Mirawara* sp., Ameletopsidae; B, *Coloburiscoides* sp., Coloburiscidae.

[M. Quick]

duce between 2000 and 12 000 eggs. Eggs of all species have unusual adhesive structures (Figs 16.4C, D), and in at least one species there appears to be an 11 month egg stage or early nymphal diapause.

Superfamily LEPTOPHLEBIOIDEA

6. Leptophlebiidae. This is the dominant family of Australian mayflies, comprising more than 50% of the described genera and about 70% of the described species; numerous genera and species remain to be described. Only the subfamily ATALOPHLEBIINAE occurs in Australia. Nymphs are dorso-ventrally flattened with prognathous heads (Fig. 16.13A–D) and variously shaped gills, usually with double lamellae, on abdominal segments 1–7 (Fig. 16.15). Adult males have their eyes divided into a large upper portion with large facets and a smaller, lower portion with smaller facets (Fig. 16.1) (Horridge and McLean 1978). In the fore wings, vein CuP is strongly recurved. The hind wings are relatively small (Figs 16.6B–D) and are absent in some exotic genera. The two tarsal claws may be similar or dissimilar.

Atalophlebia is the largest Australian leptophlebiid genus at present with 18 described species, some of which are certain to be transferred to other genera in the future. Nymphs of many species with multidigitate abdominal gills tend to be found in standing or slowly flowing waters. Several species inhabit the crevices of logs. Nymphs of many species crawl from the water before ecdysis, and although some species have adults

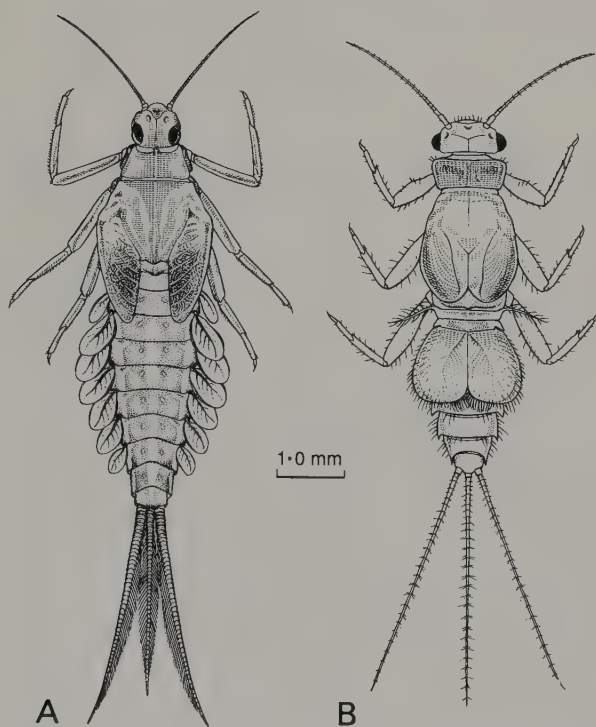


Fig. 16.12 Nymphs: A, *Centropilum* sp., Baetidae; B, *Tasmanocoenis* sp., Caenidae.

[M. Quick]

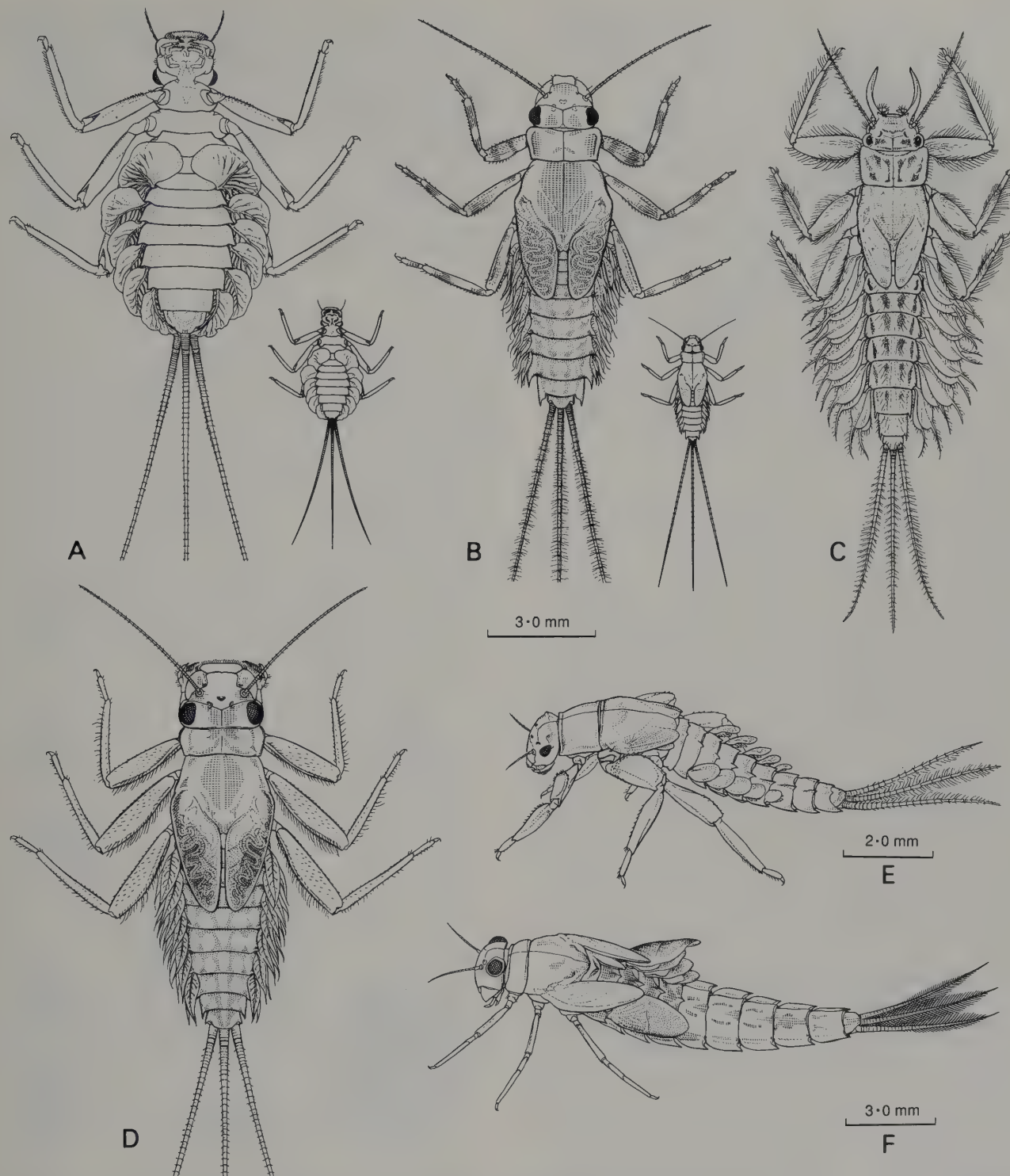


Fig. 16.13 Nymphs: A, *Kirrara* sp., Leptophlebiidae; B, *Atalophlebia* sp., Leptophlebiidae; C, *Jappa* sp., Leptophlebiidae; D, *Austrophlebioides* sp., Leptophlebiidae; E, *Ephemerellina* (*Austremarella*) *picta*, Ephemerellidae; F, *Tasmanophlebia* sp., Oniscigastridae. [M. Quick]

which swarm above the stream, it is more common for the males to patrol stretches of stream.

Atalophlebia is a widespread genus with species occurring in a range of habitats from stony upland streams and lakes, such as those in the Mt Kosciusko area, to permanent and intermittent lowland and inland streams, bill-

abongs, lakes and reservoirs. Nymphs appear to be shredders, consuming wood and leaf material (Chessman 1986). *A. australasica*, common in small, temporary and permanent streams in the Murray-Darling Basin, presumably has some mechanism for withstanding drought conditions since some of the streams in which it is abundant

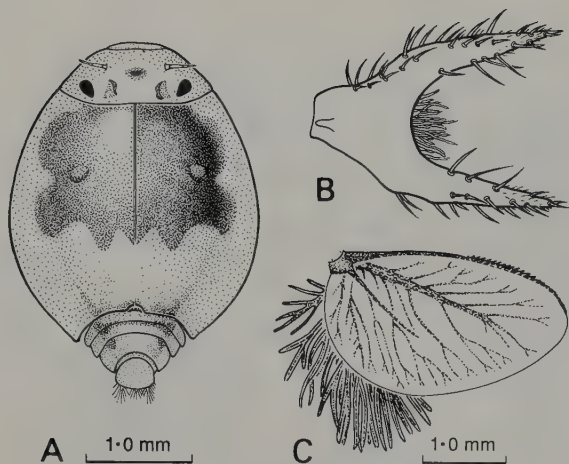


Fig. 16.14 Nymphs. A, *Prosopistoma* sp., Prosopistomatidae, dorsal aspect. Abdominal gill 4 of: B, *Coloburiscoides* sp., Coloburiscidae; C, *Mirawara* sp., Ameletopsidae. [A. Hastings]

are completely dry for more than half the year; the species is univoltine but with multiple cohorts present and adults emerge intermittently throughout the year (Suter 1980).

Austrophlebioides (Campbell and Suter 1988) includes most of the Australian species previously ascribed to *Atalophlebioides* and *Deleatidium*. Nymphs are of the sprawling type and are abundant on rocks in moderate current areas of upland streams. Adults are medium sized mayflies with completely transparent wings, and often form large swarms above streams around dusk. The genus occurs in Tas. and in streams along the eastern coast of the mainland.

Nymphs appear to be epilithic browsers (Chessman 1986) feeding on the upper surfaces of stones, mainly at night (Bailey 1981b); they are commonly collected drifting in the water (Bailey 1981a,b). Two species in a cool mountain stream near Mt Buller, Vic., are univoltine with adult emergence November–March (Duncan 1972). In the warmer La Trobe R. another species is bivoltine with a long winter and a shorter summer generation; the emergence period is February–April (Marchant *et al.* 1984).

Jappa and *Ulmerophlebia* have burrowing nymphs which are somewhat similar in appearance except that nymphs of *Jappa* possess prominent protuberances on the head. Nymphs of *Jappa* burrow in gravel and sand in stony streams (Riek 1970; Skedros and Polhemus 1986). Nymphs of *Ulmerophlebia* occur in sandy and silty areas of upland streams and in lakes (Suter 1986). Both genera appear to be absent from large, silty rivers. They feed on detritus and can also skeletonise leaves (Chessman 1986).

The 3 species currently included in *Kirrara* are not congeneric (Campbell and Peters 1986). Nymphs have greatly expanded abdominal gills forming an adhesion disc by which they anchor themselves to the tops of boulders in areas of rapid current. Adults are conspicuous because the costal and subcostal areas of the fore wings are bright orange-brown. Eggs are faceted and each facet appears to bear an adhesive structure (Fig. 16.4B).

Kirrara nymphs occur mostly in fairly warm, medium to large, upland streams on the south-eastern mainland where they browse the epilithic layers and consume both plant and animal material (Chessman 1986). The life cycle is univoltine with an adult emergence period of 3 months in early to mid-summer (Campbell and Holt 1984).

Australian *Nousia* (2 spp.) are placed in the endemic subgenus *Australonousia* (Campbell and Suter 1988); both species occur in Tasmania and *Nousia fuscula* also occurs on the mainland.

Nymphs of *Koorrnonga* (Campbell and Suter 1988) occur in a variety of habitats including riffles, pools and logs, and mostly feed on detritus and possibly also on coarse, particulate, organic material such as leaves. The genus is present in Tas. and over the whole of the eastern mainland. In a S.A. stream *K. inconspicua* is univoltine with a poorly synchronised life cycle, and adult emergence is spread over 10 months (Suter 1980). Of 2 species studied in Vic., one is univoltine, the other bivoltine with a short summer generation (Marchant *et al.* 1984). Emergence periods for both species are relatively short in spring and summer.

Garinjuga (Campbell and Suter 1988) occurs in upland streams of the south-eastern mainland, where the nymphs, with their characteristic broad gills (Fig. 16.15E) occur under stones in areas of rapid current. *Neboissophlebia* (Dean 1988) is distributed in both the south-eastern main-

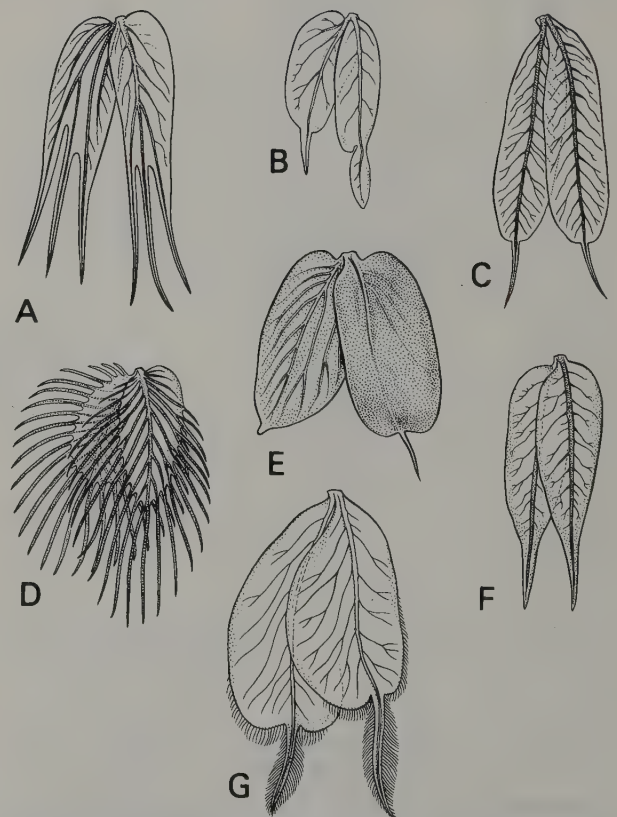


Fig. 16.15 Abdominal gills of leptophlebiid nymphs: A, *Atalophlebia australis*; B, *Choroterpes* sp.; C, *Atalophlebia yugana*; D, *A. australasica*; E, *Garinjuga maryannae*; F, *Austrophlebioides* sp.; G, *Jappa* sp. [M. Quick]

land and south-western W.A. with the nymphs feeding on leaf accumulations.

Nyungara (2 spp.) and *Bibulmena* (1 sp.) appear to be restricted to south-western W.A. where they occur in small streams in jarrah forests of the Darling Range. Nymphs of *Nyungara* resemble those of *Nousia*, while nymphs of *Bibulmena* resemble those of *Penaphlebia* from South America (Dean 1987).

Nymphs of *Atalomicria* and *Thraulophlebia* are unknown. *Thraululus* occurs in northern Australia (Grant pers. comm.) although no Australian species have yet been described.

Suborder PANNOTA

Superfamily EPHEMERELLOIDEA

7. Ephemerellidae. The single Australian species, *Ephemerellina* (*Austremerella*) *picta*, was described from a small, stony stream in southern Qld (Riek 1963; Allen 1965). Nymphs are less flattened than those of leptohebiids, and bear a prominent, double row of spines dorsally on the abdomen (Fig. 16.13E). They possess gills on abdominal segments 2–6; the dorsal portion of each gill is plate-like and the ventral portion consists of 2 rows of overlapping lobes. Adults have detached marginal intercalary veins and 1 or 2 long intercalaries between veins MP₂ and CuA in the fore wings (Fig. 16.7D).

The family is widespread in the Holarctic with genera also occurring in South America, Asia and South Africa. The subfamily in which the Australian species has been placed, *TELOGANODINAE*, is primarily Ethiopian and Oriental in distribution, and *Ephemerellina* s.str. is limited in distribution to 2 provinces in China and South Africa.

Superfamily CAENOIDEA

8. Caenidae. In Australia this family is represented by *Tasmanocoenis* (5 spp.) (Suter 1984). Like the nymphs of *Tasmanophlebia*, nymphs of *Tasmanocoenis* have an operculate abdominal gill covering the other gills, but in *Tasmanocoenis* it is the second gill rather than the first, and the operculate gills are fringed with fine hairs (Fig. 16.12B). Nymphs of *Tasmanocoenis* are also considerably smaller than those of *Tasmanophlebia*. Adults of *Tasmanocoenis* are small but distinctive; the sexes are alike, with eyes of similar size, and the hind wings are absent. The fore wings are broad (Fig. 16.7C) and fringed with fine hair (not shown in Fig. 16.7C).

Nymphs are widespread in Tas. and the mainland, occurring especially in silty areas of stony streams or

rivers, and also in standing waters. Their diet seems to consist mainly of fine detritus (Chessman 1986) and they are among the more pollution-tolerant of Australian mayflies. *T. tillyardi* in S.A. streams has 1 or 2 generations per year with multiple cohorts continuously present (Suter 1980; Suter and Bishop 1980). *T. tonnoiri* is bivoltine in the La Trobe R. while another unnamed species is univoltine (Marchant *et al.* 1984). For all 3 species the emergence period is spring-summer, and for the first 2, adults emerge for 5 months or more. In the tropical Magela Ck system, a species of *Tasmanocoenis* similar to *T. tillyardi* has a nymphal development time of about 4 weeks on average and as short as 2 weeks (Marchant 1982), with adults emerging year round.

Adults of *Tasmanocoenis* frequently swarm along the margins of streams in the early morning in temperate Australia. In tropical species swarming may occur at night at sites remote from water (Marchant 1982).

9. Prosopistomatidae. Nymphs from tropical rivers in far northern Qld (Pearson and Penridge 1980) represent an undescribed species of *Prosopistoma*. Prosopistomatid nymphs are unusual in having the mesonotum forming a carapace over the thorax and abdomen as far as segment 7 so that they superficially resemble notostracan Crustacea (Fig. 16.14A). Adults are morphologically unusual. The eyes of both sexes are small and widely separated. The fore wings have no cross-veins and the longitudinal veins in males are bordered by deep intercalaries (Fig. 16.8A); the venation of females is similar but there are no intercalaries. The fore legs of the male are barely longer than the mid and hind legs, while the legs of the female are vestigial. Females do not moult to the imaginal stage.

The family contains a single genus with a wide distribution (Africa, Madagascar, Europe, southern Asia, the Philippines, Sunda I., Sulawesi, New Guinea, Solomon Is and Australia). Adults are rarely collected because they fly before dawn for a short period only, and the taxonomy of the genus is based almost solely on the nymphs (Peters 1967). Nymphs inhabit large rivers or small streams with rubble or boulder substrata. Pearson and Penridge (1980) collected the North Qld nymphs in drift samples.

ACKNOWLEDGMENTS. This chapter is dedicated to Dr E. F. Riek who wrote the chapter in the 1st edition. We would like to thank Dr G. F. Edmunds, Jr, University of Utah, U.S.A.; Drs M. D. Hubbard, M. L. Pescador, R. W. Flowers and Mrs J. G. Peters, Florida A & M University, U.S.A.; Dr T. Soldán, Czechoslovak Academy of Sciences, Czechoslovakia; and Dr P. J. Suter, State Water Laboratory, Salisbury, S.A.; for review and helpful discussion of drafts of this chapter.

Odonata

(*Dragonflies and damselflies*)

J. A. L. WATSON and A. F. O'FARRELL

Predacious Palaeoptera with two equal or subequal pairs of wings; complex accessory genitalia developed from S2 and S3 of male. Larvae aquatic, having elongate prehensile labium modified for seizing prey, and respiring by tracheal gills developed in Australian species either as external caudal appendages or from internal folds of the rectal wall.

This ancient and unique order includes some of the world's most spectacular insects. Only about six per cent of the known species are Australian, but these include some remarkable forms. Adult Odonata usually have more or less elongate, slender bodies and highly developed powers of flight. They hunt by sight and seize their prey (flying or sessile insects) on the wing. Mostly between 30 and 90 mm long, they include some huge forms exceeding 150 mm and small, fragile species of less than 20 mm. Almost always aquatic, the larvae (often, inappropriately, referred to as nymphs) lie in wait for, or sometimes actively stalk, small animals, which are seized by shooting out the long, prehensile labium on which the palps are modified for grasping.

General accounts of the order include those of Corbet (1980, 1983) on biology and Fraser (1957), Davies (1981) and Davies and Tobin (1984, 1985) on systematics. For Australian Odonata, see Watson in Keast (1981), Watson (1982b) and Watson and O'Farrell (1985) on ecology, conservation and zoogeography, and Fraser (1960), Watson (1974, 1977a), Houston and Watson (1988) and Watson *et al.* (in press) on systematics and distribution. Rowe (1987), on New Zealand Odonata, contains much biological information on species also occurring here. Accounts of regional faunas include Watson (1962, 1969a) (W.A.), Allbrook (1979) (Tas.), Watson and Abbey (1980) (N.T.) and Hawking (1986)

(Victorian larvae). The journal *Odonatologica* abstracts the literature on Odonata.

Anatomy of Adult

Head (Fig. 17.1). Large, concave behind, on flexible, slender neck. Occipital region in female Anisoptera sometimes modified to articulate with male anal appendages in pairing. Region behind eyes in both sexes sometimes enlarged, forming postocular lobes or 'temples'. Compound eyes conspicuous as lateral swellings on transversely elongate head of Zygoptera, or more substantial, largely covering more or less spherical head of some Anisoptera. Three ocelli always present; vertex sometimes reduced to small tubercle in front of contiguous compound eyes. Antennae minute; scape relatively large, pedicel variable, flagellum thin, at most 5-segmented. Frons prominent, projecting forwards, then downwards, in front of eyes. Clypeus large, divided transversely into larger postclypeus (*nasus*) and small anteclypeus (*rhinarium*). Labrum conspicuous, sloping obliquely forwards in Zygoptera, vertical in other suborders; genae small; large areas of mandibular bases exposed. Mouth-parts (Fig. 17.2) of modified biting type, adapted for predation; wide gape, strongly toothed mandibles, spined maxillae with unsegmented palps. Labial palps modified into large lateral lobes, each bearing near apex a movable hook and spine or end-hook.

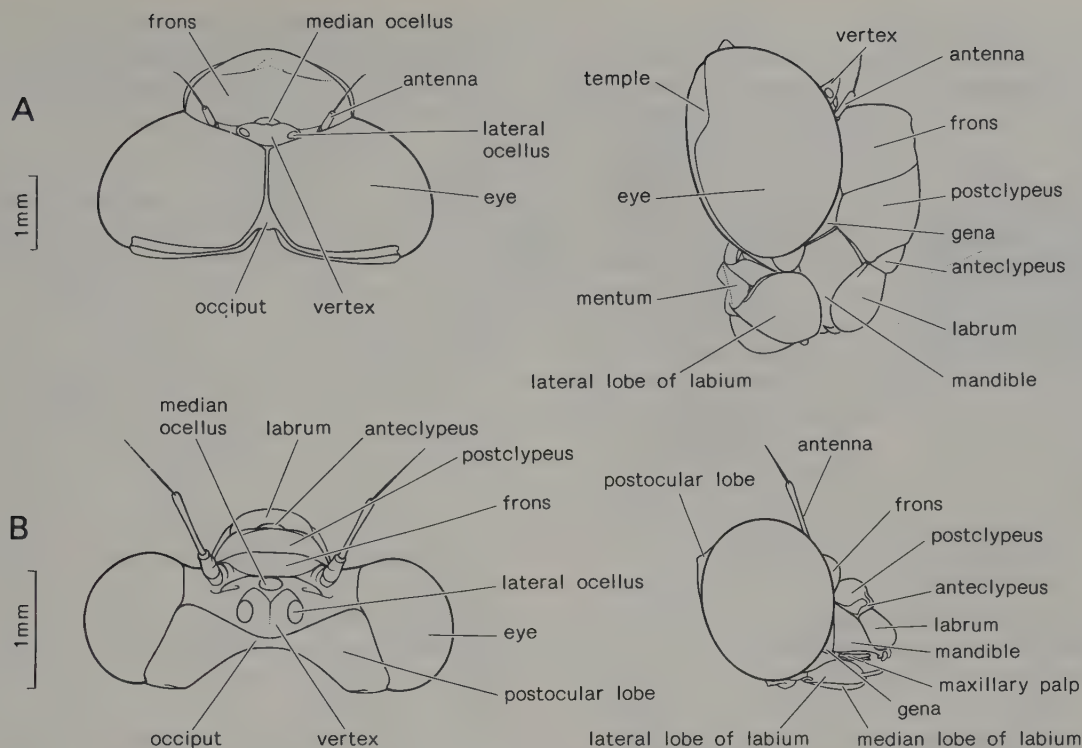


Fig. 17.1 Dorsal and lateral views of heads of ♂♂: A, *Austroaeschna parvistigma*, Anisoptera-Aeshnidae; B, *Synlestes weyersii*, Zygoptera-Synlestidae.

[F. Nanninga]

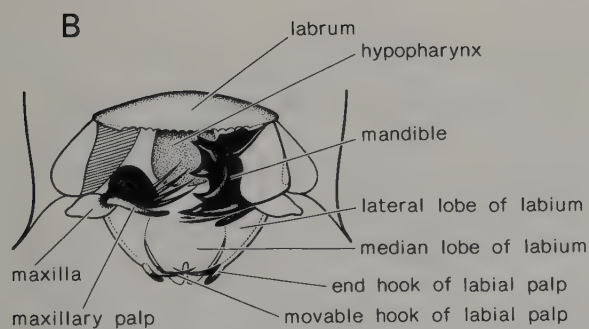
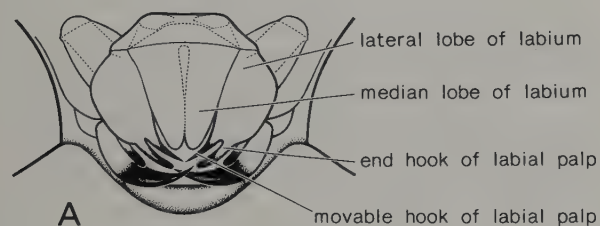


Fig. 17.2 Mouth-parts of ♂ *Synlestes weyersii*, Zygoptera-Synlestidae: A, ventral view; B, anterior view, labrum and right mandible removed.

[F. Nanninga]

Thorax (Fig. 17.3). Prothorax small, transversely elongate, mobile on large, rigid synthorax. Pronotum (modified in female Zygoptera to articulate with male appendages in pairing) often complex in shape, sometimes with prominent posterior lobe. Propleura small; mesothoracic spiracles just behind them, on anterolateral

borders of mesothorax. Meso- and metathorax fused into large rigid synthorax, with legs placed far forward and wings set well back. Sterna and nota small; region between wing-bases sloping obliquely down and backwards. Pleura huge, episterna divided into an- and katepisterna; mesanepisterna enlarged anterodorsally, meeting in mid-dorsal line along dorsal carina to form extensive 'shoulders' in front of prealar ridges. Meso-pleural (humeral) and metapleural (second lateral) sutures usually conspicuous. Interpleural (first lateral) suture, between mesepimeron and metanepisternum, sometimes obscure at dorsal end, but distinct below, with metathoracic spiracle just behind it. Katepisterna bordering coxae laterally below anepisterna.

Legs. Rather short, highly adapted for seizing and holding prey or clinging and scrambling upon a suitable perch, but not for walking. Trochanters subdivided near base; femora strong, sometimes spiny; tibiae slender, no spurs, but usually with one or more comb-like rows of spines (fused in male Corduliidae and chlorogomphine Cordulegastridae into tibial keels); tarsi 3-segmented, longest segment distal, with pair of claws, each usually armed with a tooth (claw-hook) about halfway along its length.

Wings. Humeral and axillary plates at the base of C and R+M articulating with notal sclerites of synthorax (Fig. 17.4). Wings membranous, usually hyaline, sometimes with large areas of pigment or structural colour; often with basal yellow coloration ('saffroning'). Veins and pterostigma usually black, brown or dull yellow, sometimes brightly coloured. Nearly all Anisoptera and a

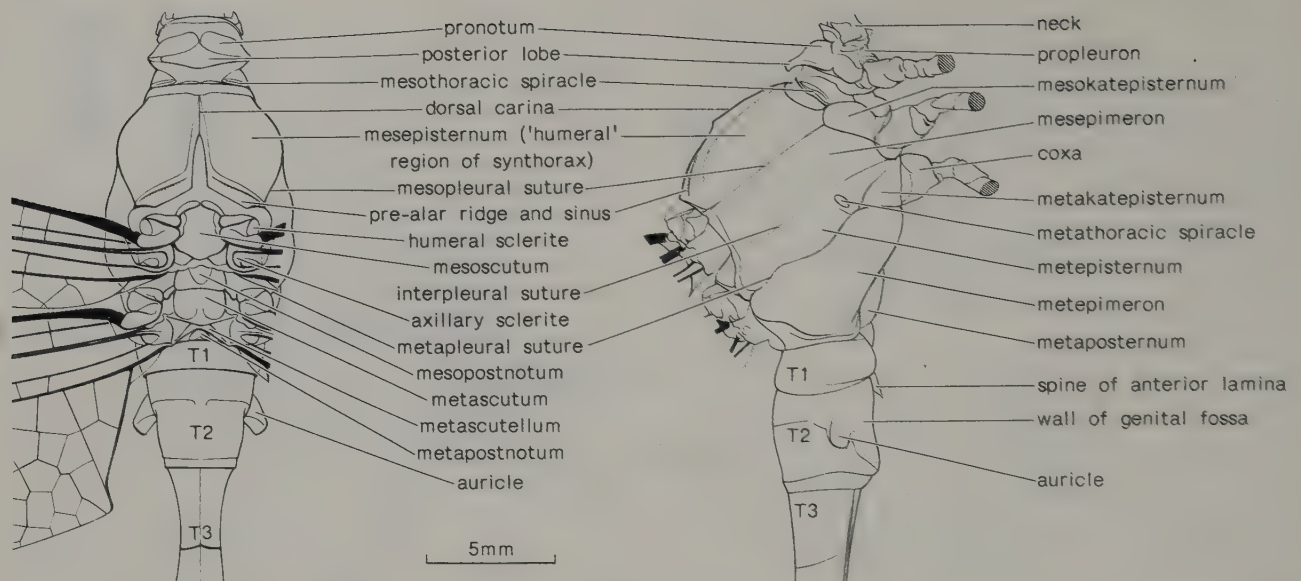


Fig. 17.3 Dorsal and lateral views of thorax and anterior abdominal segments of ♂ *Austroaeschna parvistigma*, Anisoptera-Aeshnidae.

[F. Nanninga]

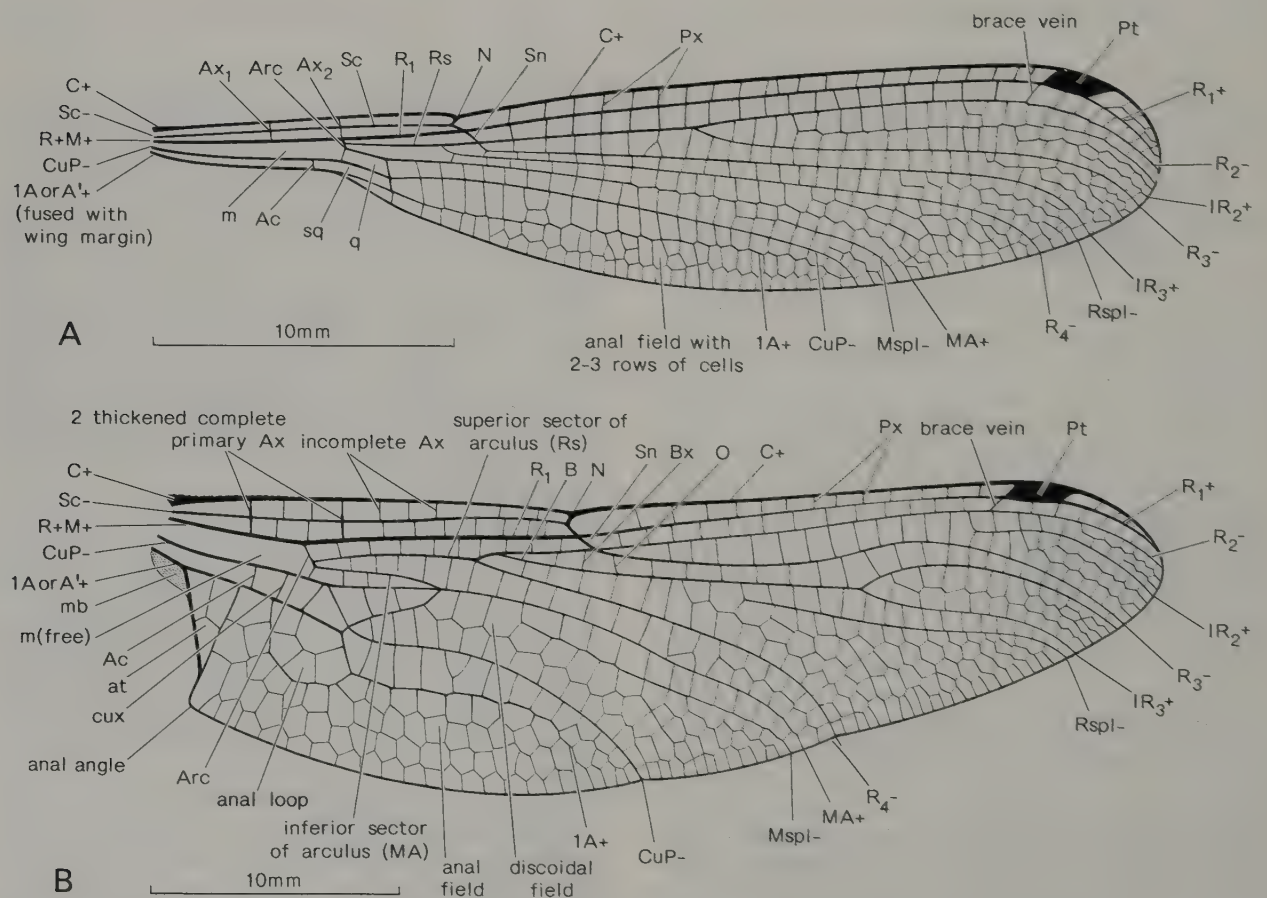


Fig. 17.4 Hind wings of ♂: A, *Austroargiolestes icteromelas*, Zygoptera-Megapodagrionidae; B, *Austroaeschna parvistigma*, Anisoptera-Aeshnidae.

[F. Nanninga]

few groups of Zygoptera resting with wings spread horizontally or somewhat depressed; others holding them vertically side by side above back, or in some intermediate position. Fore and hind wings acting independently during flight.

Venation (Fig. 17.4) complex and highly specialised. Terminology is still contentious (pp. 149–50, Figs 6.151, j). Although fossil evidence shows that it is no longer tenable (Riek and Kukalová-Peck 1984), we here retain the modified Tillyard-Fraser system used in the 1st edition and, substantially, in keys to the Australian Odonata (Fraser 1960; Watson *et al.* in press) (Table 17.1). The convex or concave position of the major longitudinal veins is indicated by + or - signs in Fig. 17.4, and in the following descriptions of the veins.

The main stems are strongly corrugated at the base of the wing: C(+) on anterior margin; Sc(-); a strong R+M(+); CuP (-, usually termed Cu₂); and 1A(+), on posterior margin of petiolate portion in Zygoptera (except *Hemiphysalia* and a few others), separate from the margin in Anisoptera. MP and CuA are regarded as absent. Sc joins C at the *nodus* (N). R₁(+), continuous with R+M, runs parallel to C, and reaches margin well beyond pterostigma (Pt). Rs+MA runs back obliquely to meet a cross-vein coming obliquely forwards from CuP, thus forming a distally convex bow, the *arculus* (Arc), straight in many Anisoptera. Rs(-) and MA(+) ('sectors of Arc') may originate from Arc separately (Fig. 17.4) or by a common stem (Figs 17.21, 23). R₂(-), parallel to R₁, is joined across R₁ to N by thick oblique *subnodus* (Sn), and often joined to inner corner of Pt by 'brace' vein. R₃(-) and R₄(-) arise pectinately from R₂, and sweep to margin behind apex. IR₂(+) and IR₃(+) are intercalary veins behind R₂ and R₃ respectively. Rsp1(-) is a secondary intercalary ('supplement') between IR₃ and R₄. IR₃ is a strong vein; its basal part, up to oblique vein 0 (Fig. 17.4B), being a proximal extension of the original larval trachea in Anisoptera, is called the *bridge* (B).

MA(+) and CuP(-), unbranched, with the supplement MASpl(-) between them, enclose the discoidal field (d), which ends proximally in the *discoidal cell* (dc) immediately distal to the posterior segment of Arc. This cell is never divided longitudinally in Zygoptera, in which it is the *quadrilateral* (q), sometimes having a *subquadrilateral* (sq) lying behind it between CuP and 1A (Fig. 17.19). In Anisoptera, CuP bends sharply backward at the base of dc, which is divided by a longitudinal cross-vein into the characteristic *triangle* (T) and *hypertriangle* (ht, Figs 17.20–23). Especially in primitive forms, T may appear four-sided, with anterior margin bent (Plate 1, B, D). If a cross-vein runs from CuP to 1A at or distal to level of Arc, it cuts off a *subtriangle* (st or ti, Figs 17.20, 21) proximal to T.

In Zygoptera, except in Lestoidea, Isostictidae and Protoneuridae (Figs 17.14, 15), in which it is greatly reduced, 1A leaves wing margin usually near distal end of petiole, and encloses a narrow anal field (a). The *anal crossing* (Ac) runs from the stem of CuP to 1A, often proximal to the departure of the latter from wing margin (Figs 17.14–19). In Anisoptera, portion of 1A proximal to Ac is sometimes designated 'A', and the vein joins or closely approaches CuP at posterior corner of T. From here, in most hind wings and some fore wings, its conspicuous anterior branch, sometimes designated 'AA', runs roughly parallel to CuP. The anal field in hind wing, usually much more extensive than in fore wing, contains, in all but some primitive forms, an *anal loop* (al, Figs 17.4B, 21) formed by a convex branch of 1A swerving back just beyond Ac and then forward again to complete the loop. In more advanced Libelluloidea, this becomes an elaborate 'stocking-shaped' formation with a strong midrib (Figs 17.22, 23). Behind 1A at extreme base of both wings, a small opaque *membranule* (mb) may occur in both sexes; and, in males only, a well-defined basal or *anal triangle* (at) may be present in hind wing (Figs 17.4B, 20, 21).

Table 17.1 Alternative terms for some features of the odonate wing

Modified Tillyard-Fraser	Riek and Kukalová-Peck	Needham	de Selys & 19th Century Workers
C	PC+CA+CP+ScA	C	Costal nervure
Sc	ScP	Sc	Subcostal nervure
R ₁	RA	R ₁	Median nervure
R ₂	RP ₁	M ₁	Principal sector
IR ₂	IR ₁	M _{1a}	Postnodal sector
R ₃	RP ₂	M ₂	Nodal sector
IR ₃	IR ₂	R _s	Subnodal sector
R ₄	RP ₃₊₄	M ₃	Median sector
MA	MA	M ₄	Lower sector of arculus
CuP (also Cu ₂)	MP	Cu & Cu ₁	Submedian nervure and superior sector of triangle
1A (also A ₁)	CuA	Cu ₂	Inferior sector of triangle
Veins of anal field	CuA+CuP+AA	A ₁ -A ₃	—
Anal border	AP	—	Anal border
Membranule	Jugal area	Membranule	Membranule

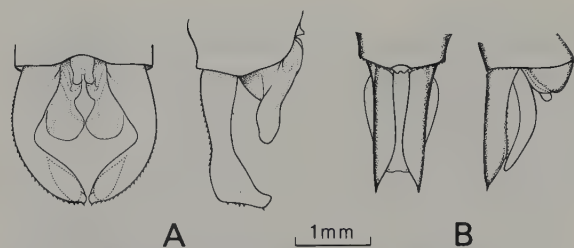


Fig. 17.5 Dorsal and lateral views of anal appendages of ♂♂: A, *Diphlebia nymphoides*, Zygoptera-Amphipterygidae; B, *Diplacodes bipunctata*, Anisoptera-Libellulidae. [F. Nanninga]

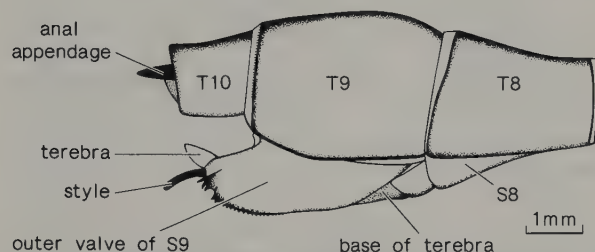


Fig. 17.6 Terminalia of ♀ *Synlestes weyersii*, Zygoptera-Synlestidae, lateral. [F. Nanninga]

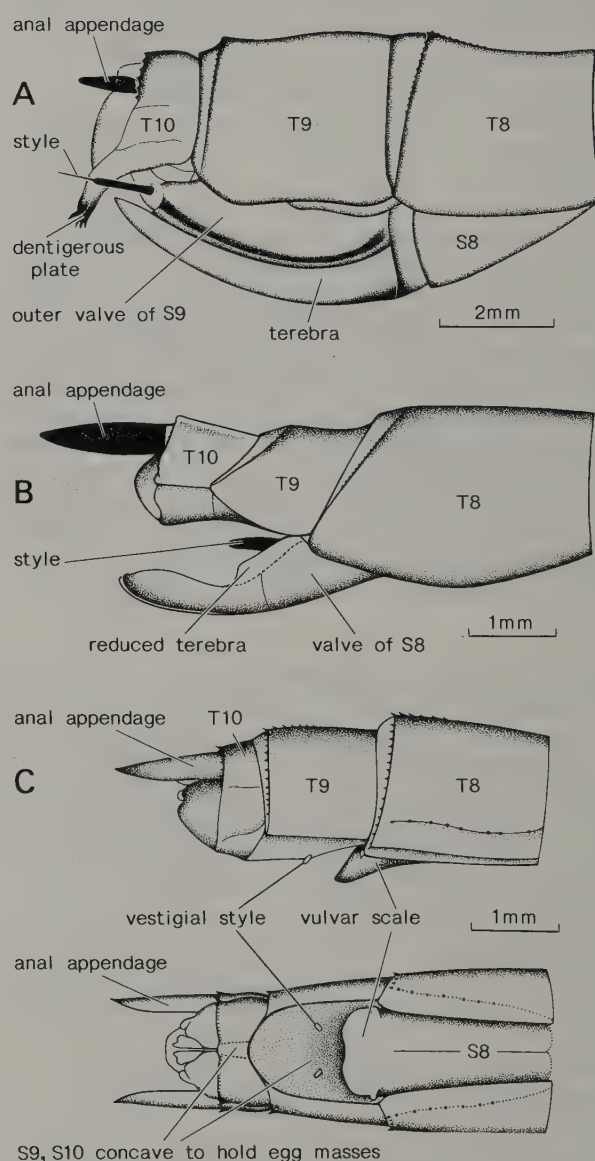
Some cross-veins are of taxonomic importance. *Antenodals* (*Ax*) join C to R_1 ('complete') or to Sc only ('incomplete') proximal to N; *postnodals* (*Px*) join C to R_1 beyond N. Number and arrangement of cross-veins *Bx* in space between R_3 , B and O; *mx* in median space (m) between R+M and stem of CuP (Fig. 17.21); *cux* in cubital space (cu) behind stem of CuP; and, if present, in at, st, T or ht, may be important. So, too, may be degree of alignment of cross-veins of different series, presence of extra intercalaries at wing margin, and number and arrangement of cells in (e.g.) discoidal or anal fields.

The venation of Odonata is specialised to cope with the aerodynamic stresses on the wings (Wootton in press). The wing is corrugated almost throughout. Transverse braces, and longitudinal pleats involving groups of veins, help to regulate bending of the wing about the nodus and, hence, to vary the degrees of pronation and supination of the basal and peripheral parts of the wing. One important bracing system involves the distal transverse veins of the quadrilateral (and, in some cases, subquadrilateral) cells and the triangle; other important braces, the primary antenodal cross-veins, strengthen the costal pleat. The discoidal field constitutes another pleat, separated from the costal pleat by the distal pleat, formed by the branches of the radial sector, R_2 – R_{4+5} .

Abdomen. Usually elongate, more or less cylindrical, often constricted at one or more points, tapered or dorso-ventrally flattened. Ten complete, flexibly articulated segments, 1–8 bearing spiracles. Terga strongly sclerotised, arched to embrace flat, narrow sterna; pleura narrow, membranous. Segments 1–2 and 8–10 or 9–10 usually shorter than rest. Males with S2–3 modified to form elaborate secondary genitalia, not homologous with paired appendages, and, in some Anisoptera, with ventrolateral outgrowths of T2 (*auricles* or *oreillets*, Figs 17.3, 8).

Segment 10 in both sexes with paired, unsegmented, superior anal appendages, probably cerci (homology disputable). Paired inferior anal appendages also present below anus in male Zygoptera; in males of other suborders, an unpaired median inferior appendage above anus (Fig. 17.5), sometimes so deeply cleft as to appear double (e.g. in some Gomphidae).

FEMALE GENITALIA (Figs 17.6, 7). Gonopore behind S8. Ovipositor complete in Zygoptera, Anisozygoptera, Aeshnidae and Petaluridae, in which gonapophyses of segments 8–9 form a cutting, piercing or sawing *terebra* ensheathed by valves of 9, which bear a sometimes segmented sensory apical style and may have cutting edges or teeth. In some aeshnids, ventral hind margin of S10 forms projecting *dentigerous plate*. Ovipositor in other Anisoptera often reduced to small, sometimes bivalved, vulvar scale; S9–10 sometimes excavated to hold egg-



S9, S10 concave to hold egg masses

Fig. 17.7 Terminalia of ♀ Anisoptera: A, *Austroaeschna pulchra*, Aeshnidae, lateral; B, *Synthemis eustalacta*, Corduliidae, lateral; C, *Diplacodes bipunctata*, Libellulidae, lateral and ventral. [F. Nanninga]

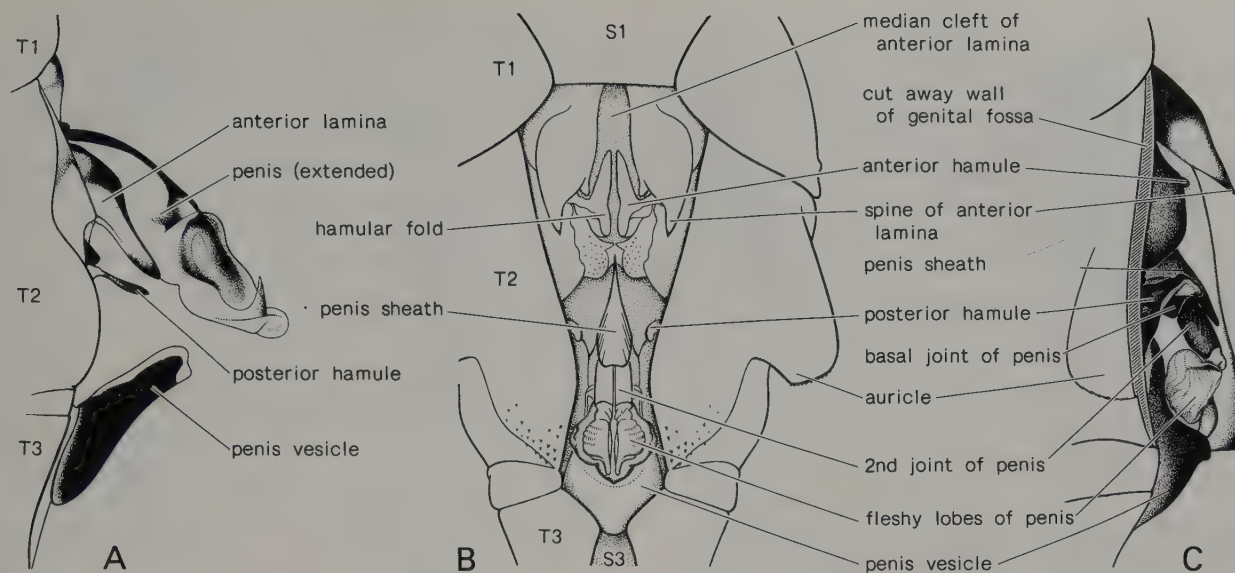


Fig. 17.8 Male accessory genitalia: A, *Synlestes weyersii*, Zygoptera-Synlestidae, lateral; B, *Austroaeschna parvistigma*, Anisoptera-Aeshnidae, ventral; C, *A. parvistigma*, from right side with right wall of genital fossa cut away. [F. Nanninga]

masses extruded from gonopore. More rarely, ovipositor only partially reduced, or functionally replaced by secondary structures.

MALE GENITALIA (Fig. 17.8). No external genitalia on segment 9, where gonopore opens. Forward ventral flexure of abdomen transfers semen to reservoir (*penis vesicle*) on anterior end of S3. S2 much modified to form *genital fossa*, within which lies the 'penis', and on either side of it clasp organs used in copulation to hold and guide female genitalia, including two pairs of processes (*hamules*), reduced to one pair except in Anisozygoptera and Aeshnoidea. 'Penis' in Anisoptera 3-segmented, with orifice on convex surface, folded with apex ventral, and partly covered anteriorly by backwardly directed *ligula* (penis sheath), pointing somewhat anteriorly when erected. Unsegmented, but otherwise similar, in Anisozygoptera. 'Penis' in Zygoptera probably homologous with anisopteran ligula, without an orifice and directed posteriorly, tip usually concealed in large penis vesicle.

Coloration. Cuticular pigments usually black, brown or dull yellow. Epidermal pigments (cream, yellow, green, blue, red) show through light or unpigmented cuticle, often in patterns of spots, stripes or bands. Metallic effects sometimes produced by structural coloration of cuticular surface; or surface covered by waxy, whitish to powder-blue secretion (pruinescence). Females often resemble immature males in colour, usually less brilliant than mature males. Especially in Coenagrionidae, there may be two or more female colour morphs—an 'andro-morph' (like mature male) and one or more differently coloured 'heteromorphs'.

Internal Anatomy. Alimentary canal long, straight; salivary glands small; long, narrow oesophagus extending into base of abdomen, there dilating into crop; gizzard small and weak in adults, but with complex internal folding and dentition in larvae; mid gut long, simple, without

caeca; hind gut short, rectum with 6 longitudinal papillae in adults, 3 in larvae. Malpighian tubules 50–70, usually arranged in groups of 5 or 6. Central and sympathetic nervous systems and retrocerebral complex well developed; brain large, optic lobes very large and complex; 3 thoracic ganglia widely separated; 1st abdominal ganglion almost fused to metathoracic ganglion, remaining 7 located anteriorly in each of abdominal segments 2–8; a ventral blood sinus associated with nerve-cord in adults, but apparently not in larvae. Respiratory system with 3 main pairs of longitudinal tracheal trunks, opening in adults by 10 pairs of spiracles, but closed in larvae. Larval mesostigma, however, well developed, often used in aerial respiration long before metamorphosis. Enormous air-sacs present in synthorax and dorsal abdomen of adults of many families. Dorsal vessel and pericardial membrane often lying beneath dorsal abdominal air-sacs, which largely conceal them from above.

Gonads elongate in both sexes, often extending when mature through abdominal segments 2–7 (ovary) or 4–8 (testis). Ovarioles panoistic, numerous; oviducts very short, leading into large spermathecal pouch, also receiving duct from accessory glands. Testes with numerous follicles, each producing radially arranged, rounded, sticky sperm-mass adapted for easy transfer from gonopore to secondary genitalia. Sperm-masses awaiting transfer stored in sperm-sac, formed by large dorsal dilation of common sperm-duct into which short vasa deferentia discharge. Filling of sperm-sac may coincide with complete development of mature coloration.

Immature Stages

Egg. Initially creamy white, usually turning red-brown within 24 hours after fertilisation. Elongate, smooth 'endophytic' eggs usually inserted into plant tissues;

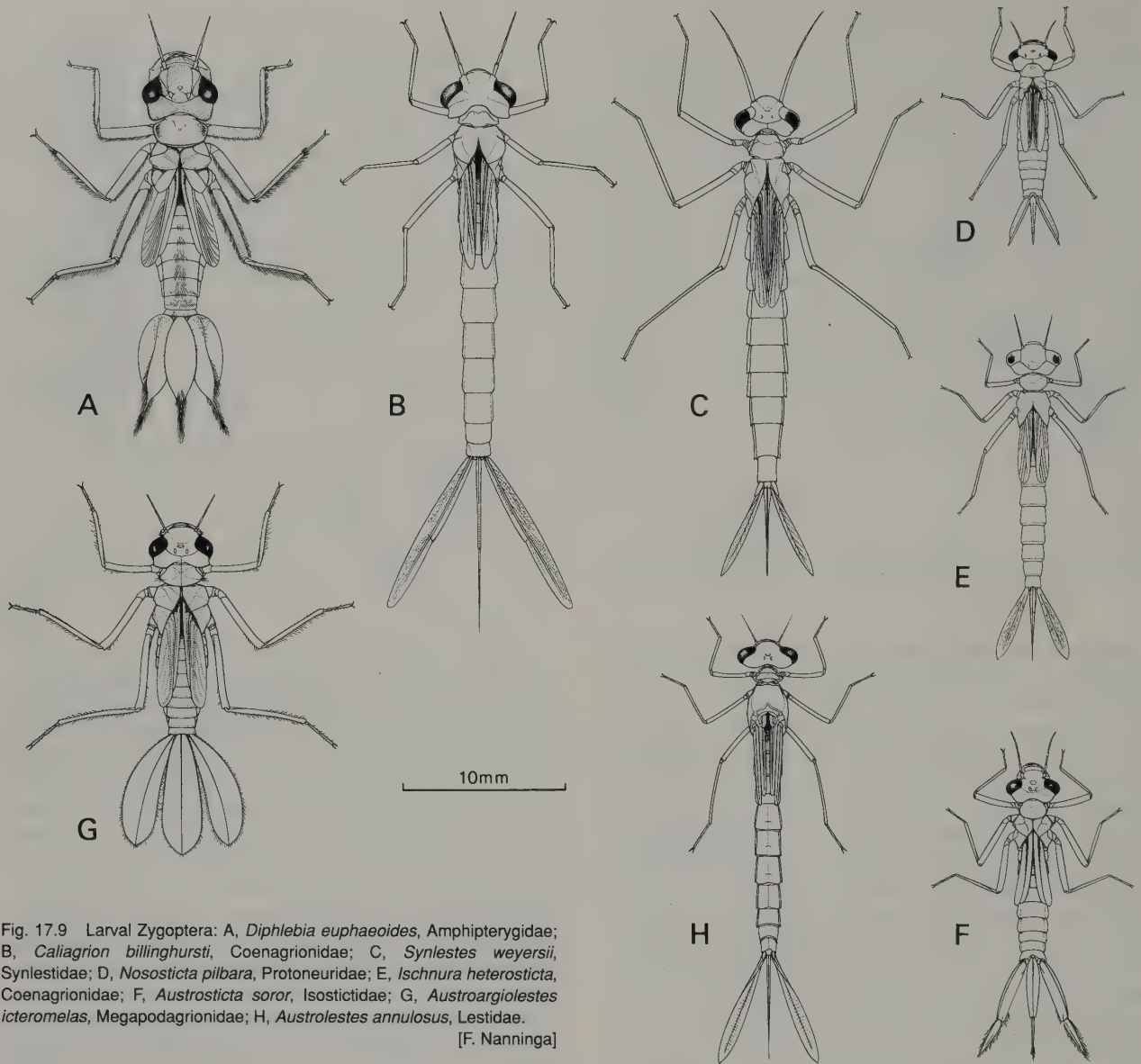


Fig. 17.9 Larval Zygoptera: A, *Diphlebia euphaeoides*, Amphipterygidae; B, *Callagrion billinghami*, Coenagrionidae; C, *Synlestes weyersii*, Synlestidae; D, *Nososticta pilbara*, Protoneuridae; E, *Ischnura heterosticta*, Coenagrionidae; F, *Austrosticta soror*, Isostictidae; G, *Austroargiolestes ictromelas*, Megapodagrionidae; H, *Austrolestes annulosus*, Lestidae.
[F. Nanninga]

ovoid or spherical 'exophytic' type, often with sculptured chorion and gelatinous investments or appendages for anchorage, usually scattered into water. Embryonic development can be regulated until after formation of germ-band; embryonic envelopes arising by invagination of germ-band into yolk. Unsegmented embryonic cuticle ensheathing folded appendages of newly-hatched 'pro-larva' sometimes retained for several minutes or longer after eclosion.

Larva. Shorter and stouter than adult, usually with relatively larger antennae, eyes smaller, always well separated (Figs 17.9, 10). Mouth-parts like those of adult, but labium (Fig. 17.11) elaborated as extensible grasping organ; labial palps adapted for seizing prey. Labium (or 'mask') hinged between pre- and postmentum, largely covering face anteroventrally. Rapidly extended by local increase in blood pressure caused by sharp contraction of abdominal and thoracic muscles, including diaphragm in abdominal segments 4–5, plus energy stored by locking

mechanism in the primary flexor muscle; returned to normal, ventrally folded position by retractor muscles. Prothorax larger and synthorax less swollen than in adult; external wing rudiments extending backwards to cover first few abdominal segments, and reversed so that hind wings overlies fore wings. Legs normally placed, adapted for walking, clinging or burrowing.

Abdomen of Zygoptera bears 3 (rarely 2) large caudal tracheal gills, often used in swimming when abdomen lashed from side to side. Gills usually plate-like (lamellate), but sometimes triangular in section (triquetral) (Fig. 17.9F) or saccoid (Fig. 17.9A); strongly constricted near centre (nodate) (Fig. 17.9F), weakly so (subnodate) (Fig. 17.9B) or denodate. They are of taxonomic value provided damaged or regenerated gills are recognised as such. Some exotic Zygoptera have segmentally arranged or perianal filamentous gills, or thin-walled lamellar ruffles on the caudal gills. In other suborders, elaborate tracheal meshwork (branchial basket) in gills on inner rectal wall

replaces external gills. Intake and expulsion of water through valves guarding anus serves for respiration and rapid propulsion. Anal pyramid (Fig. 17.12) forms spiny armature around anus; sometimes used as offensive weapon. There are 5 components: unpaired dorsal epiproct ('appendix dorsalis'), paired ventrolateral paraprocts ('cerci' of some authors), and paired dorsolateral cerci ('cercoids'), absent in very young larvae.

Female larvae show external rudiments of the ovipositor unless adult has no ovipositor, and male larvae have rudiments of genitalia on abdominal segments 2-3. In Anisoptera, 'male projection' on upper surface of epiproct is rudiment of male inferior anal appendage (Fig. 17.12A). Larval coloration usually dull; mainly cuticular pigments, sometimes brightened by underlying hues, especially greens. Pattern often distinctive, sometimes changing progressively during development, or at an ecdysis in response to environmental conditions during cuticle formation.

Biology

Adults. Of great ethological interest, adult Odonata are sometimes referred to as 'bird-watchers' insects'. They often have complex patterns of territorial, sexual and other behaviour, very largely based on visual stimuli, and the methods of the ornithologist rather than the entomologist are required to study these.

Typically diurnal, they are sometimes crepuscular and, rarely, even nocturnal. The flight season varies greatly between species, from a few weeks to many months. In temperate Australia, they fly mainly from September to April, but adults of a few species are present in winter. In the north, many more fly all year round. Little is known of the occasional migrations over long distances but some are associated with down-wind movement in frontal systems; spring-flying adults in the south-east are commonly such immigrants.

Some Odonata spend much of their active time perched, usually horizontally, on rocks, banks, twigs and

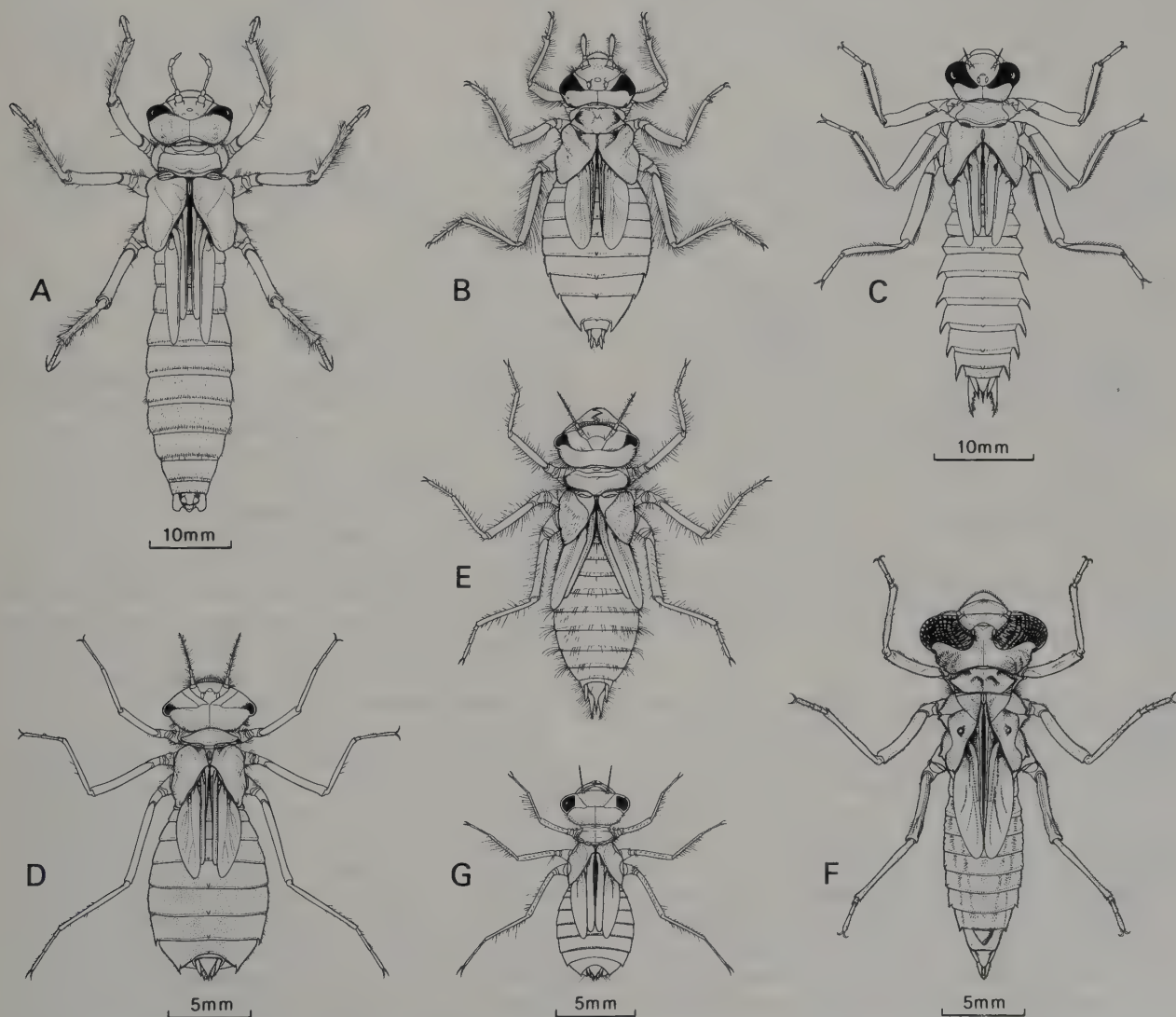


Fig. 17.10 Larval Anisoptera: A, *Petalura hesperia*, Petaluridae; B, *Austrogomphus guerini*, Gomphidae; C, *Notoaeschna sagittata*, Aeshnidae; D, *Hemicordulia australiae*, Corduliidae; E, *Synthemis macrostigma*, Corduliidae; F, *Telephlebia brevicauda*, Aeshnidae; G, *Diplacodes bipunctata*, Libellulidae. [F. Nanninga]

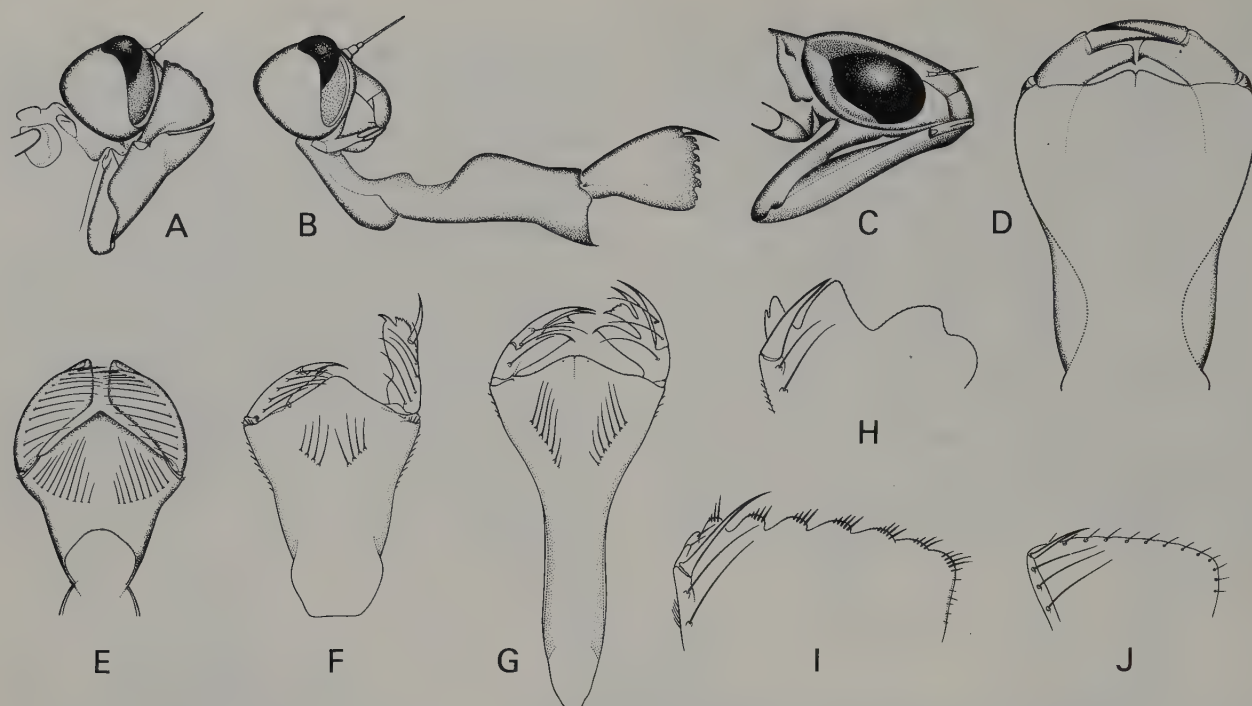


Fig. 17.11 Labia of larvae: A, B, lateral views of head of *Synthemis eustalacta*, Corduliidae, showing labium retracted and extended; C, lateral view of head, with labium retracted, of *Aeshna brevistyla*, Aeshnidae; D, dorsal view of labium of *A. brevistyla*; E, same of *Diplacodes bipunctata*, Libellulidae; F, same of *Ischnura heterosticta*, Coenagrionidae; G, same of *Austrolestes analis*, Lestidae; H, distal border of labial palp of *Synthemis macrostigma*, Corduliidae; I, same of *Hemicordulia tau*, Corduliidae; J, same of *Diplacodes bipunctata*. [F. Nanninga]

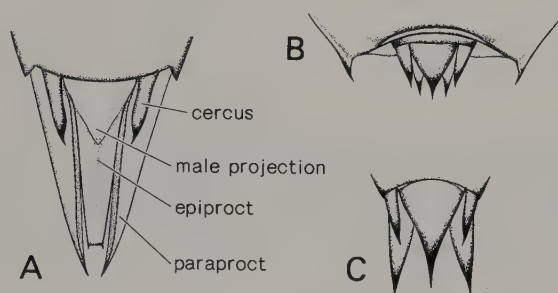


Fig. 17.12 Anal pyramids of larval Anisoptera, dorsal: A, *Aeshna brevistyla*, Aeshnidae, ♂; B, *Procordulia jacksoniensis*, Corduliidae; C, *Orthetrum caledonicum*, Libellulidae. [F. Nanninga]

the like, sallying out on short flights to feed, challenge intruders, or mate. Such 'perchers' include most Zygoptera, and the gomphids, petalurids and many libellulids among Anisoptera. In contrast, the 'fliers' remain on the wing when active, alighting, often vertically, to rest; they are principally Aeshnidae and Corduliidae, but include some libellulids (particularly Pantalinae).

Short-term, temperature-dependent physiological colour change has been reported in several families. Minute refractive bodies in the distal cytoplasm of epidermal chromatophores produce Tyndall scattering of light, against a dark background of ommochrome-laden vesicles in the proximal cytoplasm, usually giving intense blue colour, stable at higher temperatures (e.g. 20–25°C) but replaced by dull purplish-grey or black when low

temperatures (e.g. 10–16°C) induce distal migration of ommochrome vesicles. Suitable adjustment of ambient temperature and light intensity may induce several successive cycles of colour change in isolated integument *in vitro*, but central control mechanisms may also be involved. Various thermoregulatory functions may be ascribed to the dark colour phase, but adaptive functions of the bright colouring remain obscure, as do those of colour changes restricted to small areas of the body, e.g. in *Aeshna brevistyla* and *Austroargiolestes alpinus*.

Mark-recapture methods are useful in population studies on adults, if they are weak fliers uninjured by capture and show behaviour predictable enough for effective sampling. Some species may be marked and counted while roosting at night, but specialised roosting behaviour may make random sampling difficult.

Emergence commonly occurs at night, or about dawn, but may occur at other times. The 'maiden' flight, from a few to 1500 metres in length, is directed away from water. Maturation of gonads, and of adult colouring, may take days or weeks. Immature ('teneral') adults tend to avoid water; their cuticle is soft and the wings have a glassy sheen. Age may be estimated on the basis of known morphological colour change. Examination of gonads or daily growth layers of endocuticle are laboratory methods for determining adult age. Growth layers may be unusable very early or late in the adult life span.

Reproduction and Associated Behaviour. Once the pre-reproductive period is over, adults of most species return to their breeding sites. In many Zygoptera, both

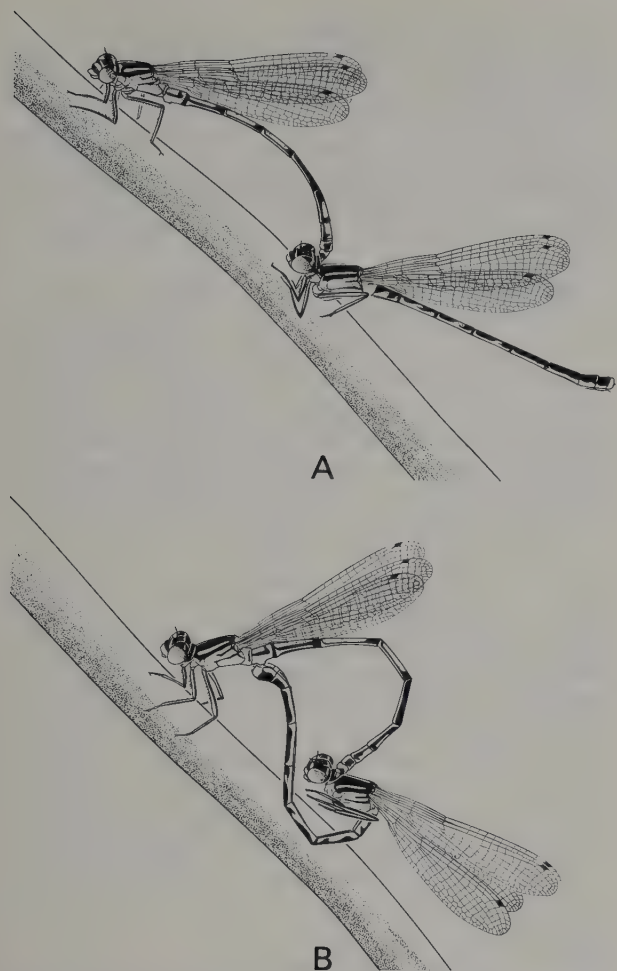


Fig. 17.13 Diagrams showing copulation in *Coenagrion lyelli*; A, tandem position; B, copulation. [S. Smith]

sexes congregate there, often in vast numbers. In most Anisoptera and some Zygoptera, females visit water only to mate and lay eggs. Males, in contrast, spend much time over or near water, in most species showing territorial behaviour which discourages intruding males of their own or, sometimes, other species. This behaviour may involve, at one extreme, simple aggression without evident attachment to a particular site, and at the other extreme, residence at a defended site for a few consecutive days, even weeks, and ritual display. Territorial perchers often have a preferred central base from which each surveys and patrols his realm, whereas fliers remain on the wing at the rendezvous.

Copulation follows rendezvous with a 'willing' female, 'reluctant' females having characteristic, negative responses. Both sexes may mate several times in one day. The accessory male genitalia are charged with semen occasionally before or, usually, immediately after seizure of the female occiput (Anisoptera) or prothorax (Zygoptera) by the male legs, then the anal appendages (the 'tandem position'). The partners then bring their genitalia in contact by flexing their abdomens (the 'wheel position') (Fig. 17.13). Prolonged flight in the 'tandem

position' without genital contact may precede and follow copulation, which may occur in flight or at rest. The male often escorts the ovipositing female; he may hold her in tandem even during underwater oviposition. Some species may attempt interspecific or homosexual matings.

The selective value of territoriality, particularly post-copulatory behaviour, depends primarily on the male's ability to displace or remove sperm provided by earlier mates and replace it with his own (Waage 1979a, 1984). A dominant male thus ensures that he excludes other males from his bailiwick; mates with as many females as he can; and guards them from intruding males while they lay the eggs that he has fertilised.

In endophytic species, eggs are inserted into tissues of submerged or emergent aquatic plants or logs, terrestrial plants on the bank, or (notably in some Aeshnidae) into soil above water but below flood level. In exophytic species, without a functional ovipositor, eggs are extruded individually or in adhesive strings or masses from the gonopore, and often washed off by the female sharply flicking the water with the tip of her abdomen or, occasionally, placing them on leaves or ground next to water. Smooth surfaces resembling water may stimulate exophytic oviposition—e.g. smooth concrete or bitumen roads.

Immature Stages. Although particular species have specialised habitats, larval Odonata occur in most environments in fresh and even brackish water, including waterfalls, torrents, permanent and intermittent streams, lakes, ponds, temporary rain pools, swamps, bogs and occasionally estuaries. Some cling to submerged plants, often preferring a particular zone; others inhabit debris and detritus, or burrow into the bottom; torrent dwellers may shelter among debris or be adapted to clinging to bare rocks. Many larvae tolerate prolonged exposure to humid air. *Podopteryx selysi* breeds in tree holes, water-filled in summer. Others, normally aquatic, can resist drying. A few species are fully terrestrial.

At least some larval Zygoptera, including species of *Coenagrion* and *Ischnura*, are territorial and defend their feeding sites; enhanced feeding can result in larger size of the resulting adults, and enhanced reproductive success of the males (Harvey and Corbet 1985).

The numbers (usually 10–15) and intervals between larval ecdyses vary widely between and within species, according to temperature, day-length, and food supply. 'Opportunist' species which colonise temporary pools, e.g. *Ischnura aurora*, *Orthetrum caledonicum*, *Diplacodes* spp., may develop from egg to adult in 8–10 weeks. Some species may take several years, but a range of 12–24 months is more usual. Diapause in eggs, larvae, and adults is well known in some Odonata, although not yet in Australian species. Larval diapause may result in simultaneous emergence of adults in localities where the season favourable for reproduction is brief.

Metamorphosis commences days or weeks, even months, before the final ecdysis. The epidermis retracts progressively from the distal parts of the larval labium; the large, pigmented, compound eyes of the adult develop; feeding ceases; the wing-buds swell; and shortly

before emergence, the pharate adult protrudes its head and anterior thorax above the water surface, and starts to breathe through the mesothoracic spiracles.

When metamorphosis is complete, the pharate adult crawls from the water, up an emergent plant, rock or bank, anchors itself firmly by its tarsal claws, and the imago emerges.

Natural Enemies. Fish, frogs, reptiles and birds prey heavily on larvae and on teneral and ovipositing adults. Often themselves voracious cannibals, larvae and adults are also attacked by a wide variety of other predatory arthropods. Hymenopterous egg parasites, ectoparasitic aquatic mites, parasitic worms (including trematodes of aquatic birds) and sundry micro-organisms are also associated with Odonata. Chironomid larvae sometimes attach themselves to larval Odonata (Hawking and Watson 1990).

Although human activities have not yet endangered any Australian species of Odonata, the position of *Hemiphysalia* remains uncertain, and exploitation of isolated, fresh water refuges may pose threats. Adults of some stream-dwelling Odonata, on the other hand, have potential as monitors of water quality.

Economic Significance. There is inadequate evidence to assert that Odonata play a major part in 'biological control' of other insects, although considerable larval and adult predation occurs. Edible fish, notably trout, some aquatic game birds, and (in parts of Asia) humans feed extensively on larvae and adults. The larger larvae may attack young fish, including trout fry, but are themselves used as bait; and some large adults cause damage by preying on honey bees.

Special Features of the Australian Fauna

The level of endemism is high in Australian Odonata. The Hemiphysalioidea, Lestoideidae, chorismagrionine

Synlestidae and cordulephyine Corduliidae are endemic, as are most or all genera of Isostictidae, Megapodagrionidae, Synlestidae, brachytrone Aeshnidae, Neopetaliidae, Petaluridae and gomphomacromiine Corduliidae. Only in Coenagrionidae, Lestidae and Libellulidae of the major families are few genera endemic. The widespread families Platycnemididae, Platystictidae and Cordulegastriidae are lacking, and the superfamily Calopterygoidea is very poorly represented.

Adult Odonata can be found throughout Australia, including the inland, but they are most abundant and diverse in the wet tropics and along the warmer parts of the coastal and montane east. Watson (1974) summarised the distributions of Australian dragonflies. The richest faunas are those of north-eastern Qld and Cape York, totalling more than 150 species; only 27 are known from Tas. The Odonata of Cape York and the Kimberley region are relatively poorly known.

Australia has a high proportion of stream-dwelling Odonata, primarily south-western and eastern montane. Many of these, plus a few others, can be interpreted as southern, possibly Gondwana, relicts—the Synlestidae, Gomphinae (Gomphidae), Neopetaliidae, Petaluridae, Gomphomacromiinae and Synthemistinae (Corduliidae) plus, perhaps, *Pentathemis membranulata* and the Brachytroneinae, totalling about 40% of the fauna. The existence of endemic, cold-water genera in Tas.—*Archipetalia* (Neopetaliidae) and *Synthemistops* (Synthemistinae)—and south-western Australia—*Armagomphus* (Gomphinae) and *Hesperocordulia* (Gomphomacromiinae)—implies long isolation of stream faunas there, as do some isolated species-groups in the south-west.

On the other hand, some groups have northern affinities; many are still-water forms. Substantial tropical groups include coenagrionids, perhaps isostictids, protoneturids, anactine and gynacanthagine aeshnids, and libellulids, again about 40% of our fauna.

CLASSIFICATION

Order ODONATA (302 Australian spp.)

Suborder ZYGOPTERA (107)

HEMIPHYSALIOIDEA (1)

1. Hemiphysalidae (1)

COENAGRIONOIDEA (55)

2. Coenagrionidae (30)
3. Isostictidae (14)
- Platycnemididae (0)
- Platystictidae (0)
4. Protoneturidae (11)
- Pseudostigmatidae (0)

LESTOIDEA (44)

5. Lestidae (14)
6. Lestoideidae (2)
7. Megapodagrionidae (21)
- Perilestidae (0)
- Pseudolestidae (0)
8. Synlestidae (7)

CALOPTERYGOIDEA (7)

9. Amphipterygidae (5)
10. Calopterygidae (1)
11. Chlorocyphidae (1)
- Dictyristidae (0)
- Euphaeidae (0)
- Polythoridae (0)

Suborder ANISOZYGOPTERA (0)

Epiophysalidae (0)

Suborder ANISOPTERA (195)

AESHNOIDEA (87)

12. Aeshnidae (43)
13. Gomphidae (38)
14. Neopetaliidae (2)
15. Petaluridae (4)

CORDELEGASTROIDEA (0)

Cordulegastriidae (0)

LIBELLULOIDEA (108)

16. Corduliidae (53)
17. Libellulidae (55)

The order of families within superfamilies, and of subfamilies in the entries for families, is alphabetical.

We believe that the great majority of the Australian

species have now been recognised, although some may still be accorded only subspecific status.

KEY TO THE AUSTRALIAN SUBORDERS OF ODONATA

Fore and hind wings similar in shape and usually in venation; discoidal cell quadrangular, never longitudinally divided; ♂ inferior appendages paired, below anus. Larvae usually slender, with 3 (exceptionally only 2) large caudal gills ZYGOPTERA

Fore and hind wings dissimilar in venation and usually in shape; discoidal cell divided longitudinally into 'triangle' and 'hypertriangle'; one median inferior appendage in ♂, above anus. Larvae stout, without caudal gills, but with an anal pyramid..... ANISOPTERA

The Anisozygoptera, with living representatives in Japan and the Himalayas, have the facies of Anisoptera but zygopteran-like venation (although the discoidal cell is broader in the hind wing than the fore). The gomphid-like larva has 5-segmented antennae when fully grown.

Subfamilial classification of the Coenagrionidae and Libellulidae is unsatisfactory, and the subfamilies that, e.g., Fraser (1957) and Davies (1981) recognised cannot readily be diagnosed. They are, therefore, omitted from the keys that follow. Keys to larvae are tentative, as so many larvae are unknown, and apply only to the last-stage.

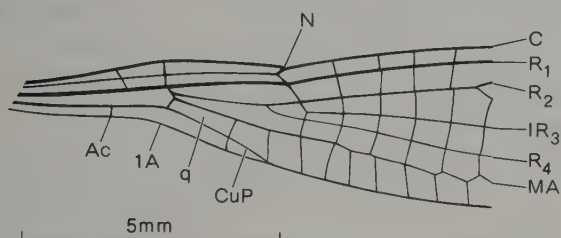


Fig. 17.14 Base of hind wing of *Nososticta solida*, Protoneuridae.

[F. Nanninga]

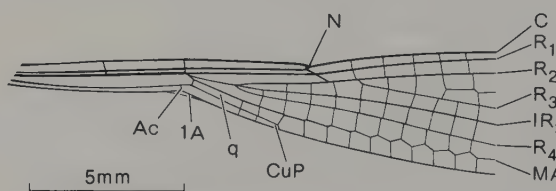


Fig. 17.15 Base of hind wing of *Lestoidea barbara*, Lestoideidae.

[F. Nanninga]

Suborder ZYGOPTERA

Keys to the Families and some Subfamilies of Australian Zygoptera

ADULTS

1. Normally 2 antenodal cross-veins, both extending across costal and subcostal spaces (Figs 17.14–18) 2
Several antenodal cross-veins, the extra veins not necessarily extending across both costal and subcostal spaces (Fig. 17.19) 11
- 2(1). Anal vein vestigial or absent, so that there are no longitudinal veins behind CuP beyond the discoidal cell (Figs 17.14, 15) 3
Anal vein long, straight or zigzagged, extending well beyond level of subnodus (Figs 17.16–18) 5
- 3(2). Anterior sector of arcus (Rs) forking about a third to half of the way from arcus to level of subnodus (Fig. 17.15) **Lestoideidae**
Anterior sector of arcus forking well beyond half-way from arcus to subnodus, sometimes beyond subnodus (Fig. 17.14) 4
- 4(3). Black marked with cream, green, blue or orange; CuP 2 cells or less long, commonly 1 cell **Protoneuridae**
Pale brown to dark greenish grey, rarely black, thorax and abdomen sometimes pruinose; CuP of variable length, 1–several cells long **Isostictidae**
- 5(2). Arculus of fore wing missing, so that discoidal cell is open at base 6
Arculus of fore wing normal, discoidal cell closed at base 7
- 6(5). CuP strongly arched forward in first cell after it leaves posterior distal corner of discoidal cell (cf. Fig. 17.18) **Synlestidae-CHORISMAGRIONINAE**
CuP almost straight in first cell beyond discoidal cell **Hemiphlebiidae**
- 7(5). No supplementary longitudinal veins between branches of Rs (R₂, IR₂, R₃, IR₃ and R₄) in distal part of wing **Coenagrionidae**
At least 1 supplementary, intercalated vein between branches of Rs in distal part of wing 8
- 8(7). Anterior sector of arcus (Rs) forking less than half-way from arcus to level of subnodus (Fig. 17.17) **Lestidae. 9**
Anterior sector of arcus forking well beyond half-way from arcus to level of subnodus (Fig. 17.4A) 10
- 9(8). Discoidal cells similar in shape in fore and hind wings **LESTINAE**
Discoidal cell of hind wing conspicuously longer than that of fore wing **SYMPECMATINAE**

- 10(8). CuP strongly arched forward in first cell after it leaves posterior corner of discoidal cell (Fig. 17.18) **Synlestidae-SYNLESTINAE**
 CuP almost straight in first cell beyond discoidal cell (Fig. 17.4A) **Megapodagrionidae**
 11(1). Only the 2 basal antenodal cross-veins extending across both costal and subcostal spaces, the additional cross-veins confined to the costal space (Fig. 17.19) **Amphipterygidae** 12
 Numerous antenodal cross-veins in both the costal and subcostal spaces 12
 12(11). Abdomen much longer than wings; pterostigma absent **Calopterygidae**
 Abdomen shorter than wings; pterostigma present **Chlorocyphidae**

LARVAE

1. Median caudal gill reduced to a spine **Chlorocyphidae**
 Median gill lamellate, laterals triquetral **Calopterygidae**
 Median and lateral gills similar in form 2
 2(1). Movable hook of labial palp armed with setae (Fig. 17.11G) **Lestidae**
 Movable hook of labial palp lacking setae 3
 3(2). Gills saccoid, sharply pointed, lacking node 4
 Gills saccoid, triquetral or lamellate, pointed or rounded at tip, nodate or, if lamellate, often denodate 5
 4(3). Gills about half as long as rest of body (Fig. 17.9A); outer margin of labial palp with row of short, stout setae **Amphipterygidae**
 Gills about quarter length of rest of body; outer margin of labial palp with basal tuft of long setae **Lestoideidae**
 5(3). Labium with paraglossae; small, approximately 14 mm or less long **Hemiphlebiidae**
 Paraglossae absent; various sizes 6
 6(5). Median lobe of prementum cleft in midline 7
 Median lobe entire, or with vestigial cleft 8
 7(6). Gills short, lamellate, denodate, held with edges uppermost (Fig. 17.9C) **Synlestidae**
 Gills elongate, either lamellate and held horizontally (Fig. 17.9G) or triquetral, with or without long terminal filament beyond node **Megapodagrionidae**
 8(6). Gills nodate, strongly constricted at node (Fig. 17.9F) **Isostictidae**
 Gills denodate or subnodate, scarcely constricted at node (Fig. 17.9B) 9
 9(8). Gills denodate (Fig. 17.9D); 1 pair premental setae **Protoneuridae**
 Gills subnodate or denodate; 1-many pairs premental setae **Coenagrionidae**

Superfamily HEMIPHLEBIOIDEA

1. Hemiphlebiidae. The tiny, metallic green *Hemiphlebia mirabilis*, the only member of the superfamily, has an enigmatic mixture of primitive and apparently reduced larval and adult features. Feared to be extinct, it is now known to survive in swamps on Wilsons Promontory in Vic.

Superfamily COENAGRIONOIDEA

2. Coenagrionidae. Adults typically skim low over still or sluggish waters where larvae live among aquatic plants. Few are endemic. The mainly tropical AGRIOCNEMIDINAE includes some of the world's smallest Odonata in the large genus *Agriocnemis* (6-7 Australian spp.). The tiny, long-legged *Austrocnemis* (3 spp., north and east, 1 extending to New Guinea) perch on floating leaves, and the much larger, dull red to black *Argiocnemis rubescens* is common on north and east coast streams.

AMPHICNEMIDINAE (the blue and black *Archibasis mimetes* and the extremely slender, orange-red *Teinobasis rufithorax*) occur on tropical streams. The widespread, south-eastern *Coenagrion lyelli*, blue and black, is the only Australian representative of the cosmopolitan COENAGRIONINAE. Females of the world-wide ISCHNURINAE have a mid-ventral spine on S8, and some species are heteromorphic in coloration. Australian species include the slender, northern *Aciagrion fragilis* and 2 of

our commonest and most widespread Zygoptera—*Ischnura heterosticta* (males blue and black) and the much smaller *I. aurora* (males extensively red), which ranges from Asia to the South-West Pacific and is windborne, occurring on oceanic islands and desert waterholes. The subfamily PSEUDAGRIONINAE includes 2 monotypic genera, the common red, blue and black *Xanthagrion erythroneurum*, which can form vast

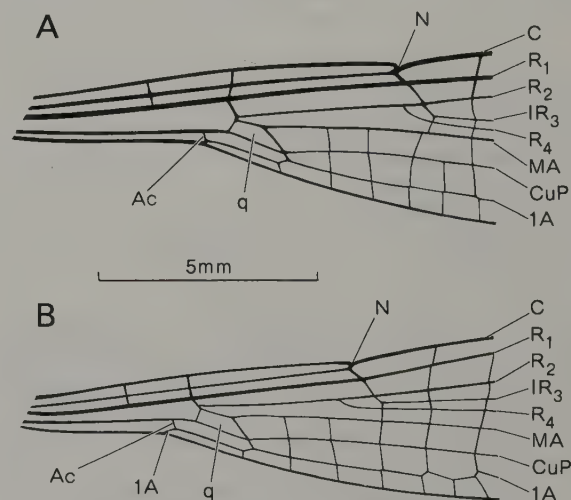


Fig. 17.16 Bases of hind wings of Coenagrionidae: A, *Pseudagrion ignifer*; B, *Ischnura heterosticta*. [F. Nanninga]

colonies on inland waters, and the large, blue and black, endemic, south-eastern *Caligrion billinghami*, distinguished by the proximal position of Ac. The bright to dull red *Ceragrion aeruginosum* is common in the north. *Pseudagrion* (5 spp., north and east) includes *P. ignifer*, dark, pruinose, the male yellow-faced, on streams; *P. aureofrons*, with spectacular blue and gold male (Plate 1, K); *P. cingillum* and *P. microcephalum*, the males blue and black; and a very large, dully coloured, northern species. The widespread genus *Austroagrion* (4 spp., all small, 2 extending beyond Australia), probably antecedent with Coenagrioninae, has blue and black males.

3. Isostictidae. Slender, dully coloured, confined to Australia, New Guinea and New Caledonia. The Australian species are stream dwelling or riverine. Short superior appendages in the male distinguish the northern and eastern *Rhadinosticta* (2 or 3 spp.; CuP short) previously placed in the New Caledonian *Isosticta*, and the 2 northern *Austrosticta* (CuP long, as in the monotypic northern *Lithosticta* in which superior appendages as long as inferiors). Superior appendages longer than inferiors in *Neosticta* (3 spp., CuP long) and 3 genera with CuP short: *Eurysticta* (3 spp., N.T. and North W.A.), the very slender *Oristicta filicicola* (North Qld) and the large *O. vallisii* (North Qld to Vic., not closely related to *O. filicicola*) (Watson *et al.* in press).

4. Protoneuridae. All Australian species are now placed in *Nososticta* (11 spp.; Watson and Theischinger 1984b), north-western to eastern, most stream-dwellers but some riverine; slender, hovering, black marked with orange, dull yellow or shades of blue or green, some with brown-banded or yellow wings. *N. solida* (Plate 1, I) is widespread in eastern Australia. Some N.T. and north-western species have very restricted ranges.

Superfamily LESTOIDEA

5. Lestidae. Typically still-water damselflies. The northern *Lestes concinnus*, resting with wings partly open, is our only species of LESTINAE. The SYMPECMATINAE, resting with wings closed, includes the Australia-wide *Austrolestes*, comprising 10 bronze or black species marked with blue (Plate 1, H), and 3 northern species of *Indolestes*, duller in colour; *I. obiri* frequents caves and overhangs. No genera are endemic. [Watson and Moulds 1979]

6. Lestoideidae. The systematic position of the endemic and only genus, *Lestoidea* (2 spp., North Qld), is unresolved. The cubital and anal venation is reduced, but the wing is lestid or megapodagrionid in other ways. The larva is amphipterygid-like, but lacks perianal gill tufts.

7. Megapodagrionidae. Only ARGIOLESTINAE occur in Australia. The northern *Podopteryx selysi*, at over 90 mm span our largest damselfly, breeds in tree holes. Theischinger and O'Farrell (1986) revised the 10 species of the endemic genus *Austroargiolestes*, most stream-dwellers, all eastern, resting with wings spread. The relationships among the remaining 10 species, placed in *Argiolestes*, are poorly understood. Not congeneric with typical *Argiolestes* from New Guinea, some breed in

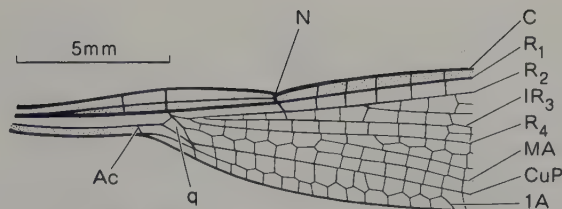


Fig. 17.17 Base of hind wing of *Austrolestes cingulatus*, Lestidae.
[F. Nanninga]

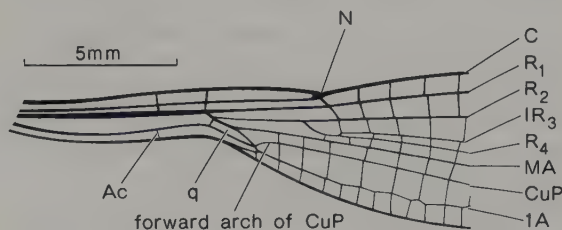


Fig. 17.18 Base of hind wing of *Synlestes weyersii*, Synlestidae.
[F. Nanninga]

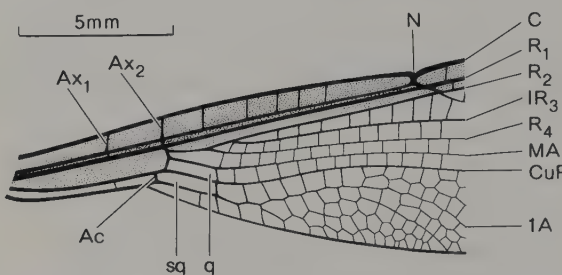


Fig. 17.19 Base of hind wing of *Diphlebia nymphoides*, Amphipterygidae.
[F. Nanninga]

streams, others in bogs or seepages; all hold the wings open. Members of the south-western *A. pusillus* complex (Watson 1977b) are the smallest *Argiolestes* (span sometimes below 30 mm), and can breed in summer-dry swamps.

8. Synlestidae. The endemic *Chorismagrion* (1 sp., North Qld) (CHORISMAGRIONINAE) has no close relatives. *Episynlestes* (3 spp.; Theischinger and Watson 1985), and *Synlestes* (3 spp.) represent the SYNLESTINAE, confined to the east, including the *S. weyersii* complex, often regarded as including 3 species (Plate 1, F). All Australian synlestids breed in streams.

Superfamily CALOPTERYGOIDEA

9. Amphipterygidae. Our only genus, *Diphlebia*, includes 5 robust, eastern species, resting with wide-open wings, the males vivid blue and black (Plate 1, E), the females dull (Stewart 1980). *D. euphaeoides* extends to New Guinea. The stout larvae (Fig. 17.9A) live in fast streams.

10, 11. Chlorocyphidae, Calopterygidae. *Rhinocypha tinctoria* and *Neurobasis australis*, respectively, are alleged to represent these families in northern Australia, but no material has been reported this century.

Suborder ANISOPTERA

Keys to the Families and some Subfamilies of Australian Anisoptera

ADULTS

1. Compound eyes widely separated on top of head 2
 Eyes close together on top of head or, most commonly, narrowly or broadly fused in midline 4
- 2(1). Male with broad, leaf-like superior anal appendages; female with complex ovipositor bearing pair of styli near tip, which extends to or beyond end of abdominal segment 10 **Petaluridae**
 Male superior appendages relatively slender, more or less rounded in section; ovipositor reduced to scale-like structure rarely extending beyond end of abdominal segment 9, and lacking styli **Gomphidae**. 3
- 3(2). Triangle of fore and hind wing traversed by cross-veins; hind wing more than 33 mm long **ICTINOGOMPHINAE**
 Triangle of fore and, usually, of hind wing entire; hind wing shorter than 33 mm **GOMPHINAE**
- 4(1). Triangle of fore wing elongate along wing axis (Fig. 17.4B) 5
 Triangle of fore wing not elongate along wing axis, often elongate across it (Fig. 17.23) 9
- 5(4). Anterior part of both wings marked with series of rounded, reddish brown spots **Neopetalidae**
 Anterior part of wings colourless except for pterostigma, or marked with brown stripe, sometimes sub-divided into bands and broad, rounded nodal spot **Aeshnidae**. 6
- 6(5). MA unbroken distally and running parallel to, or diverging from, R_4 (Fig. 17.4B) **BRACHYTRONINAE**
 MA degenerate distally and converging upon R_4 7
- 7(6). Anal appendages very long and thin; ♀ dentigerous plate a 2- or 3-pronged digging-fork **GYNACANTHAGINAE**
 Anal appendages and dentigerous plate not as above 8
- 8(7). R_3 smooth distally; anal triangle in hind wing of ♂ well developed **AESHNINAE**
 R_3 kinked forward distally; anal triangle absent **ANACTINAE**
- 9(4). Cross-veins present in median space (Fig. 17.21) **Corduliidae-SYNTHEMISTINAE**
 No cross-veins in median space (Fig. 17.22) 10
- 10(9). Basal side of hind wing triangle far beyond arculus, separated from it by a distance equal to or greater than the length of the arculus 11
 Basal side of hind wing triangle nearer to arculus, up to approximately half the length of arculus beyond it, often in line with it 13
- 11(10). Large species, hind wing more than 35 mm long **Corduliidae-MACROMIINAE**
 Small species, hind wing less than 35 mm long 12
- 12(11). Sectors of arculus separating closer to arculus than to first cross-vein beyond it; male with auricles and angulated base to hind wing **Corduliidae-CORDULEPHYINAE**
 Sectors of arculus separating abruptly close to first cross-vein beyond arculus; male lacking auricles, hindwing rounded at base **Libellulidae** (pt)
- 13(10). Sectors of arculus fused at their origins and forming a short stalk (except in the fore wing of some *Rhyothemis*); wing coloration variable, often with dark general, nodal or distal pigmentation (including *Rhyothemis*) **Libellulidae** (pt)
 Sectors of arculus diverging from their origins (at least in fore wing); wings hyaline or partly suffused yellow or pale orange, with or without yellow to reddish brown marks at their bases 14
- 14(13). Basal side of hind wing triangle at or slightly basal to arculus; anal loop stocking-shaped, expanded, with extra cells, at tip (not necessarily in *Metaphya*) **Corduliidae-CORDULIINAE**
 Basal side of hind wing triangle slightly to well beyond arculus; anal loop compact to sausage-shaped, not expanded, and without extra cells, at tip (except occasionally in *Hesperocordulia*) **Corduliidae-GOMPHOMACROMIINAE**

LARVAE

It is often difficult to distinguish larval Corduliidae from Libellulidae.

1. Labium flat, shallow, lying below head when closed (Fig. 17.11C); prementum lacking setae (Fig. 17.11D) 2
 Labium deeply concave, ladle-shaped, palps much broadened, covering face when closed (Fig. 17.11A); prementum armed with setae (Fig. 17.11E) 5
- 2(1). Antennae 4-segmented; fore tarsi 2-segmented **Gomphidae**
 Antennae 6–7 segmented; all tarsi 3-segmented 3
- 3(2). Labial palp with small spine at base of movable hook; median lobe of prementum sharply triangular **Petaluridae**
 No small spine at base of movable hook; median lobe rounded, with or without marginal denticles 4
- 4(3). Abdominal segments with broad, rounded to triangular lateral lobes, lacking on 9 **Neopetalidae**
 Some abdominal segments, including 9, with sharp lateral spines (Figs 17.10C, F) **Aeshnidae**
- 5(1). Labial palps toothed distally (Figs 17.11H, I); anal pyramid short; cerci usually at least half as long as paraprocts (Fig. 17.12B) **Corduliidae**
 Labial palps not toothed distally (Figs 17.11E, J) or, if toothed, then anal pyramid is long; cerci usually less than half as long as paraprocts (Fig. 17.12C) **Libellulidae**

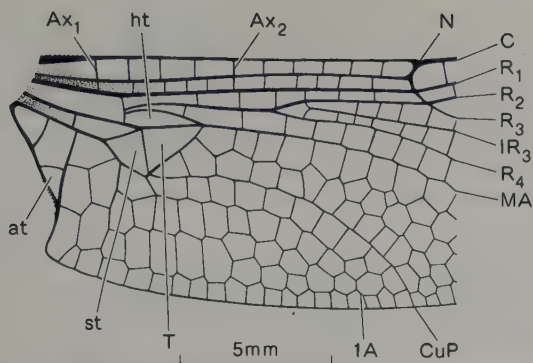


Fig. 17.20 Base of hind wing of *Austrogomphus guerini*, Gomphidae.
[F. Nanninga]

Superfamily AESHNOIDEA

12. Aeshnidae. With 8 genera, all endemic, and 30 species the subfamily BRACHYTRONINAE dominates Australia's large aeshnid fauna. All but one species are restricted to the east; most breed in streams. The median space is crossed in *Dendroaeschna* (1 sp.) and in the crepuscular *Antipodophlebia* (1 sp.) and *Telephlebia* (6 spp.; Theischinger 1985; Plate 1, G), the last two with semi-terrestrial or terrestrial larvae. *Austroaeschna* (16 spp., 1 western) is the largest genus, and *Notoaeschna* and *Spinaeschna* each have 2 spp. (Theischinger 1982). *Acanthaeschna* and *Austrophlebia* are monotypic, tending to crepuscular; spanning 120–150 mm, the latter is our largest aeshnid. *Anax* (3 northern spp.), the common, widespread *Hemianax papuensis*, and the northern *Anaciaeschna jaspidea*, annectent with the Aeshninae, represent the ANACTINAE. All breed in still waters. So do the crepuscular GYNACANTHAGINAE, with 5 dully coloured, tropical species of *Gynacantha*, *Agyrtacantha dirupta* and the more brightly coloured and widely distributed *Austrogynacantha heterogena*, none endemic genera. The widespread *Aeshna brevistyla*, our only representative of the cosmopolitan AESHNINAE, breeds in mainly still, permanent waters. Aeshnid larvae are elongate and unmistakable (Figs 17.10C, F).

13. Gomphidae. Most gomphids are black and yellow dragonflies. The 3 large, northern species of *Ictinogomphus* represent the ICTINOGOMPHINAE, breeding in still or sluggish waters. The GOMPHINAE includes 2 groups. The first comprises *Antipodogomphus* (6 spp., north and east, larvae with elongate abdomen) and *Austrogomphus* (19 spp. in 5 subgenera, widespread, larval abdomen short) (Plate 1, C; Fig. 17.10B), each with a ventrobasal branch on male superior appendage; most breed in flowing water, but some in tarns and inland river pools. Genera in the second group, *Hemigomphus* (7 spp., north and east), *Armogomphus armiger* (W.A.) and *Odontogomphus* (2 spp., North Qld) have forcipate superior appendages and a modified S11 in the male; all breed in flowing water. Gomphid larvae (Fig. 17.10B) are bottom-dwellers, often burrowers. [Watson 1991]

14. Neopetaliidae. The archaic *Austropetalia patricia* (south-eastern mainland) and *Archipetalia auriculata*

(Tas.) have their only living relatives in South America, *Austropetalia* and the South American *Phyllopetalia* being very close.

15. Petaluridae. The only Australian genus, the endemic *Petalura* (4 spp., Qld, N.S.W., W.A.) includes one of the largest living Odonata, *P. ingentissima*, wingspan more than 160 mm. The thickset larvae (Fig. 17.10A) are semiaquatic, living in burrows in swamps and beside streams.

Superfamily LIBELLULOIDEA

16. Corduliidae. Australia has a rich and highly endemic corduliid fauna. The endemic subfamily CORDULEPHYINAE comprises the eastern genus *Cordulephya* (4 spp.) (Plate 1, D), small, black and orange-yellow, resting with wings closed, the larva with deeply dentate distal margin of the labial palp. The cosmopolitan CORDULINAE includes 4 Australian genera. The monotypic, northern *Pentathemis* has affinities in South America and Madagascar. *Metaphya tillyardi* occurs in New Guinea and some adjacent Australian islands. *Procordulia* (2 spp., south-west and south-east) and *Hemicordulia* (9 spp.), neither endemic, are better known. *H. australiae* and *H. tau* are almost ubiquitous; *H. tau* is an opportunist, colonising temporary and permanent waters, and sometimes migrates in swarms. The Australian GOMPHOMACROMIINAE comprises 14 species in 8 endemic genera,

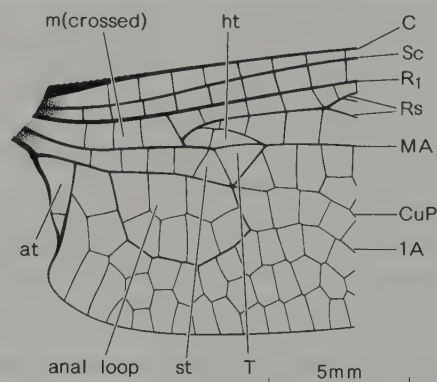


Fig. 17.21 Base of hind wing of *Synthemis eustalacta*, Corduliidae.
[F. Nanninga]

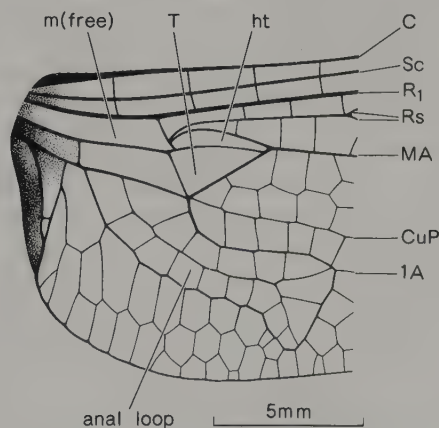


Fig. 17.22 Base of hind wing of *Procordulia jacksoniensis*, Corduliidae.
[F. Nanninga]

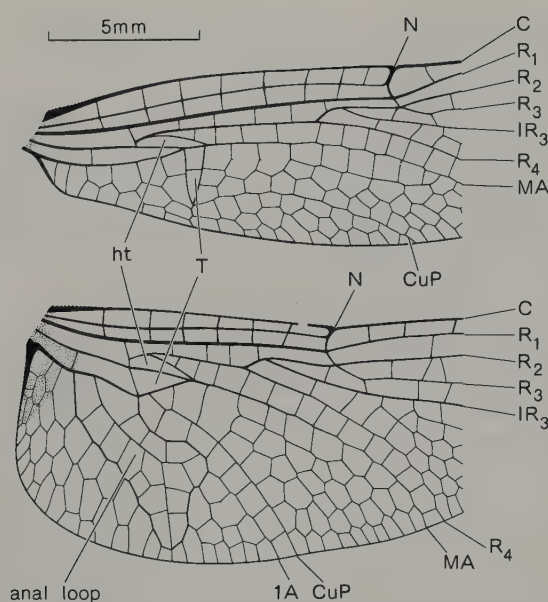


Fig. 17.23 Base of fore and hind wings of *Diplacodes bipunctata*, Libellulidae. [F. Nanninga]

3 monotypic, including *Hesperocordulia* in the south-west (Theischinger and Watson 1978, 1984). *Apocordulia macrops* and, to some extent, *Austrocordulia refracta* are crepuscular. Larval *A. refracta* can withstand drying; larvae of, apparently, *Pseudocordulia* are terrestrial and, like *Archaeophya*, resemble Synthemistinae in lacking setae on the distal margin of the labial palp. Two robust, tropical species of the almost cosmopolitan *Macromia* represent the MACROMIINAE, with very long-legged, spidery larvae in streams and rivers. Confined to the South-West Pacific, the SYNTHEMISTINAE is our largest corduliid subfamily (19 spp. in 4 genera, 2 endemic). *Synthemopsis* (monotypic, Tas.) has dark nodal spots in all wings. The endemic genus *Choristhemis* (3 eastern spp.) is not readily distinguished from *Synthemis* (10 spp., including 4 in the south-west, 3 without close eastern counterparts). *Eusynthemis* (5 eastern spp.) has very short male anal appendages, and the female lacks an ovipositor; 3 species have more or less distinct subspecies. Synthemistine larvae are bottom-dwellers in swamps and streams, and some withstand desiccation; their wing-sheaths diverge (Fig. 17.10E), and the labial palps lack setae on their distal margin.

17. Libellulidae. Although the Libellulidae is the largest family of Australian Odonata, it is less dominant than in many countries, and endemism is low. Many

species are brightly coloured. There are 3 Australian genera of BRACHYDIPLACTINAE: *Brachydiplax* (2 northern to eastern species); *Raphismia* (*R. bispina* in far North Qld); and *Nannophya* (Plate 1, B) (4 tiny, bog-dwelling species, in the south-west, east and north, including *N. pygmaea*, which ranges to Japan). LIBELLULINAE are well represented in still waters, particularly northern, with *Orthetrum* (7 spp., including the common *O. caledonicum*, male powder-blue), *Agrionoptera* (2 spp.), *Lathrecista* (1 sp.) and the endemic *Notolibellula* (1 sp.). PANTALINAE (4 genera) are broad-winged, strong fliers. *Pantala flavescens*, dull yellow, is circumtropical and temperate. *Trapezostigma* (= *Tramea*) (4 spp.), red, with red 'saddle-bags' in the base of the hind wing, extends over much of the mainland. *Hydrobasileus* (1–2 spp.), black marked with yellow, and *Camacinia othello*, very large with darkly patterned wings, are northern; *Hydrobasileus* ranges down the east coast into N.S.W. RHYOTHEMISTINAE include 5 species of *Rhyothemis*, all short-bodied with broad, beautifully pigmented wings, and mainly northern, although *R. graphiptera* and *R. phyllis* occur in N.S.W. SYMPETRINAE are well represented. *Diplacodes* (5 spp.) dominates, *D. bipunctata* (male red and black) and *D. haematodes* (male scarlet) being common and widespread. The northern *Nannodiplax rubra*, tiny and *Nannophya*-like, and the larger *Rhodothemis lieftincki* (male red) extend into N.S.W.; *Crocothemis nigrifrons* (male deep powder-blue and black) comes farther south, east and west. *Neurothemis* (2 northern spp.) includes the common *N. stigmatizans* (male with red wings), the first dragonfly described from Australia. *Tetrathemis* (1 sp.) and *Nannophlebia* (3–4 spp.) represent the primitive TETRATHEMISTINAE, small, black and yellow species with narrow wings, primarily stream-dwelling in the north and east. *Austrothemis nigrescens*, red and black, the only species in an endemic genus of TRITHEMISTINAE, has a broad, southern distribution but is very local. The UROTHEMISTINAE (= Macrodiplactidae of Fraser 1957, 1960), with sparse, open venation, includes *Aethriamanta* (2 red spp., north and north-east) and the larger, red *Urothemis aliena*, northern, both with large, secondary ovipositor. *Macrodiplax cora*, orange-yellow and black, lacking ovipositor, is a widespread northern vagrant. The crepuscular *Zyxomma* (3 spp.) and *Tholymis tillarga* (ZYXOMMATINAE) are primarily tropical, *Z. elgneri* and *Tholymis* ranging into South-East Qld; *T. tillarga* is widespread in the Old World.

ACKNOWLEDGMENTS. We thank Professor P. S. Corbet and Mr G. Theischinger for their helpful comments on the draft of this chapter.

Plecoptera

(Stoneflies)

G. THEISCHINGER

Mandibulate exopterygote Neoptera, with two, subequal pairs of membranous wings; larvae almost all aquatic.

The Plecoptera is a small order of aquatic insects with a world total of little more than 2000 species. They occur across all continents except Antarctica and from sea level to an altitude of about 5600 m (in the Himalayas). They are soft bodied, four-winged, rather uniform in appearance and vary in length from 4 to 50 mm. Adults of most species are fully winged (maximum wing span about 110 mm); some are brachypterous and apterous forms are known in several genera.

Plecoptera are superficially similar to and share some primitive character states with Orthoptera and Embioptera. They differ from Orthoptera in wing venation and in the more equal texture of fore and hind wings, by having only three tarsal segments, and by usually having aquatic larvae with tracheal gills. They can be distinguished from Embioptera by their unspecialised fore tarsi, distinctive wing venation, mouth-parts structure and by having ocelli. Plecoptera do not show close phylogenetic relationships with any other neopterous group and possibly they are the sister group of the Neoptera as a whole.

The literature on world Plecoptera up to 1972 is covered in three catalogues (Claassen 1940; Illies 1966; Zwick 1973). Comprehensive treatments of parts of the Australian stonefly fauna are those of Hynes (1978) on the larvae of Vic., Hynes (1981, 1982) and Hynes and Bunn (1984) on larvae and adults of Tas. and W.A. and Theischinger and Cardale (1987) on the adults of all Australian species. Michaelis and Yule (1988) catalogued the Australian species.

Anatomy of Adult

Head. Sessile on broad prothorax; prognathous; gula absent; epicranial and frontoclypeal sutures sometimes absent. Compound eyes well developed; usually 3, rarely 2 ocelli. Antennae long, slightly tapering, multisegmented. Mouth-parts completely formed, sometimes weak; mandibles well formed in all Australian species, vestigial in some extralimital groups; each maxilla well developed, with galea, lacinia and 5-segmented palp; labium complete, with large submentum, prementum sometimes divided, glossae, paraglossae and 3-segmented palp.

Thorax. The 3 segments free; prothorax large and mobile with wide, flat, undivided notum and undifferentiated pleuron; meso- and metathorax subequal, each with prescutum, scutum, scutellum and postnotum, pleura divided into episternum and epimeron, sterna complete except that spinasternum missing from metathorax; spiracles normally placed.

Legs. Coxae short; trochanters small; femora long, strong, more or less flattened; tibiae slightly longer than femora, with 2 small apical spurs in all Australian species except Eustheniidae which have 1; tarsi 3-segmented with simple, strong, paired claws and an empodium.

Wings. Membranous, generally similar, with hind wing larger than fore wing; when folded usually projecting beyond apex of abdomen; often reduced in length, exceptionally completely absent; coupling apparatus absent. Venation in primitive taxa rich, with numerous cross-veins; in most families reduced (Figs 18.5A-G). M origi-

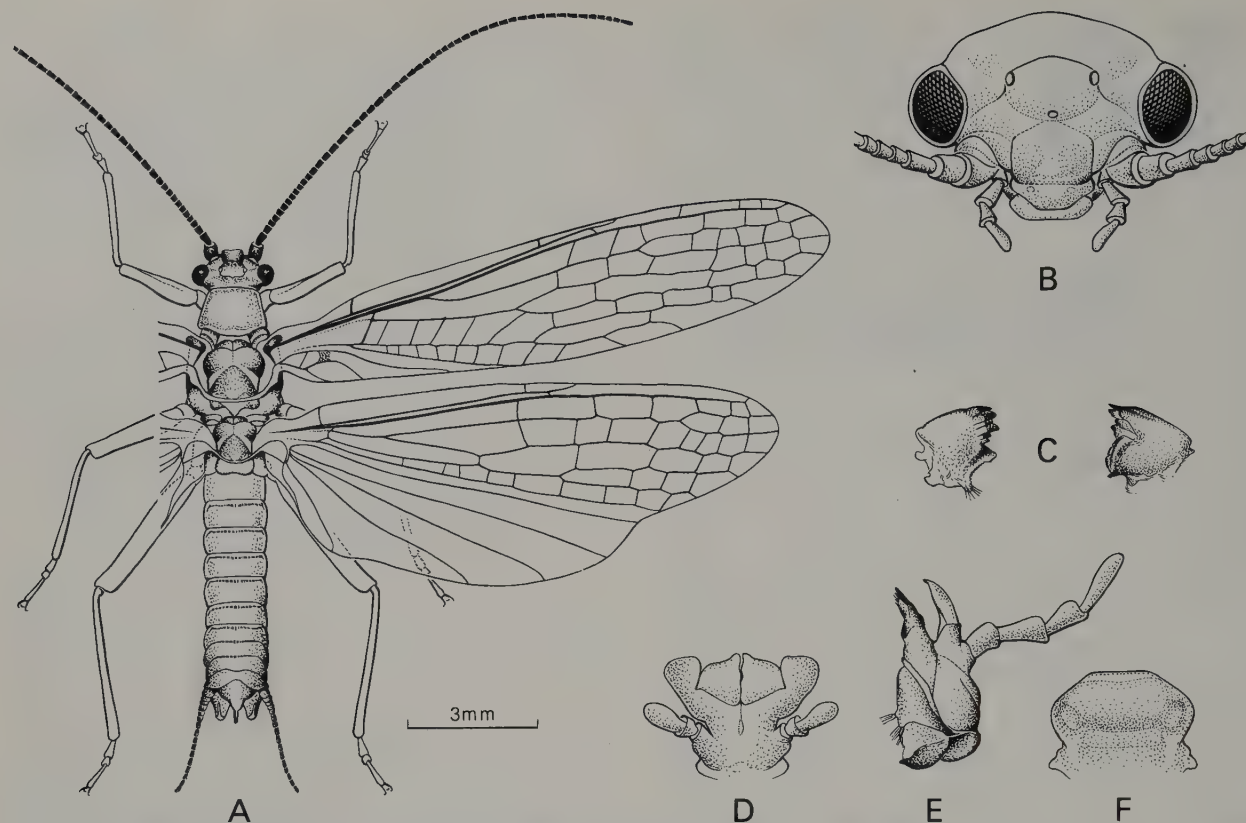


Fig. 18.1 Adult *Illiesoperla* sp., Gripopterygidae: A, habitus; B, head; C, mandibles; D, labium; E, maxilla; F, labrum.

[T. Binder]

nating from base of wing in fore wing, from Rs in hind wing. 1A in fore wing of a few Australian Eustheniidae distinctly raised and sclerotised; small, but conspicuous sclerotised patch present between 1A and 2A in many Antartoperlaria. In repose, wings normally folded closely over dorsum, with anal area of hind wing folded fan-wise against body, and one fore wing closely enwrapping all but basal portion of the other.

Abdomen. Soft, cylindrical or somewhat flattened; 10 distinct segments and vestiges of segments 11 and 12. Spiracles on segments 1–8. Female gonopore opening on or behind S8; S7, S8 or S9 usually modified to form subgenital plate or ovipositor. Male with gonopore opening behind undivided S9. No appendicular copulatory organ, but a secondary structure developed from an eversible genital chamber and sometimes incorporating paired penis rudiments. Segment 10 usually a complete annulus in female, sternite often reduced and membranous in male. Segments 11 and 12 represented by paraprocts (subanal lobes), cerci and epiproct (supra-anal lobe) all of which, together with S9 and T10, are often modified and function in males as accessory copulatory organs. Males of some Arctoperlaria with drumming lobe, hammer or hair brush(es) on one or several posterior sternites.

Internal Anatomy. Oesophagus very long; gizzard rudimentary or absent; mid gut small; hind gut short; 2 pairs of salivary glands; 20–100 Malpighian tubules. Brain and suboesophageal ganglia small; stomatogastric system normal; 3 thoracic ganglia; primitively with 8

abdominal ganglia, but sometimes reduced by fusion to 5, 6 or 7. Tracheal system opening to exterior by 2 pairs of thoracic and 8 pairs of abdominal spiracles. In male, pair of testes, each composed of several follicles, usually joined, forming arch-like structure; separate vasa deferentia communicate with pair of seminal vesicles and end in median ejaculatory duct, or (less usually) remain paired up to the gonopore. In female, ovaries composed of many

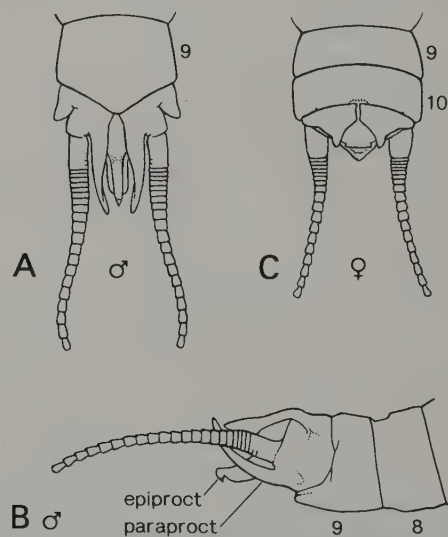


Fig. 18.2 Terminalia: A, male, ventral; B, male, lateral; C, female, ventral.

[M. Quick]

panoistic ovarioles and either separate or ovarioles arise from common duct joining oviducts of each side; spermatheca usually present, exceptionally a bursa copulatrix.

Immature Stages

Egg. Of very variable shape, 0.18–0.80 mm long and 0.13–0.60 mm wide in Australian species; usually with an outer coating which swells markedly and becomes sticky when moistened, with additional adhesive structures in many Arctoperlaria. Chorion, if sclerotised, presents good specific characters.

Larva. Generally similar to adult, but without fully developed wings or genitalia (Figs 18.3, 6). Many species with simple, flat or cylindrical gills set individually or tufts of gills set on a common stock, on mentum, submentum, neck, thorax, abdomen, anal region or bases of legs. Remnants of larval gills in adults usually important in classification. Australian Arctoperlaria have abdominal or anal gills; Australian Notonemouridae lack gills.

Biology

Adults. Generally, stoneflies are found only near fresh water, usually by running streams or lakes, especially in high country. They blend well with the substrate on which they rest. Many hide under loose bark of trees and logs. They are rather clumsy fliers, but most run well. They may be collected in the morning or during dull days as they emerge on rocks protruding from the streams, or at other times by beating foliage along the stream margin. Many Australian Gripopterygidae and *Stenoperla* are attracted to artificial lights at night. One apterous species of Capniidae passes its whole life history in the depths of

Lake Tahoe, U.S.A. Most Australian stoneflies emerge at about dawn, larger species (Eustheniidae, Austroperlidae, *Eunotoperla*, *Illiesoperla*, *Trinotoperla*) in the dark, smaller species often in the morning hours. Most larger species apparently fly straight up into the tall trees soon after emergence. Short-winged species cannot fly but climb to the top of vegetation. *Eusthenia* and *Thaumatoperla*, when disturbed, raise their wings to appear larger and some species display striking colours to discourage enemies. Adults of all families of Australian stoneflies feed on green algae, lichen, bark, rotten wood, higher plant tissue (possibly detrital) and diatoms. Austroperlidae and Eustheniidae eat rotten wood which seems essential for egg production. *Stenoperla*, which has fully-developed eggs in the last larval instar and lays eggs within 2–3 days of emergence, eats very little. The life span in captivity of Australian species is 5–50 days, females living longer than males. In the south-east of Australia all Austroperlidae, some Eustheniidae, some Notonemouridae and almost all Gripopterygidae appear in spring and early summer. Most Notonemouridae emerge from late autumn to early spring and only a few Eustheniidae and Notonemouridae and very few Gripopterygidae are definite autumn species. There is marked autumn emergence (after the rainy season) of Gripopterygidae in tropical Qld (Hynes 1976b; Theischinger 1984; Yule 1985).

Reproduction. Most stoneflies mate during daylight; a few nocturnal species only at night. Drumming (tapping upon the substrate with the tip of the abdomen), a species-specific communication prior to mating in many Arctoperlaria, is unknown in Australian stoneflies. Little courtship prior to mating has been observed, but the striking and species-specific colours of some Australian Eustheniidae may be for species recognition. During mating the male is superimposed on the female. For oviposition females of some Australian Gripopterygidae and of *Stenoperla* glide down to the water surface where extruded eggs are washed from the tip of the abdomen. *Eusthenia* and *Thaumatoperla* crawl under water, *Eusthenia* spreading the eggs in a layer on the underside of stones, *Thaumatoperla* dropping a solid mass of eggs of almost cherry size. Eggs of some Notonemouridae with long ovipositors are placed deep in wet, rock crevices. Eggs may be laid singly, in one batch or in several batches and may total between 100 and more than 1000 per female. Coated and sticky eggs are usually laid in masses on the underside of stones and logs, whereas uncoated eggs (possibly all Australian Gripopterygidae) lie loose in the substratum. Many Australian species appear to oviposit in the dark (Hynes 1976b; Zwick 1980, 1981a).

Immature Stages. Embryonic development generally takes between a few weeks and one year. In times of severe drought the eggs of the Australian *Dinotoperla bassae* may remain in diapause for 18 months or more. *Austrocercia tasmanica* and *Austrocercella hynesi* (Notonemouridae), a few Gripopterygidae and several Northern Hemisphere Nemouridae lay fully-eyed ova (ovoviviparity). Larvae require cool, well-aerated water. Growth and development takes from several months to

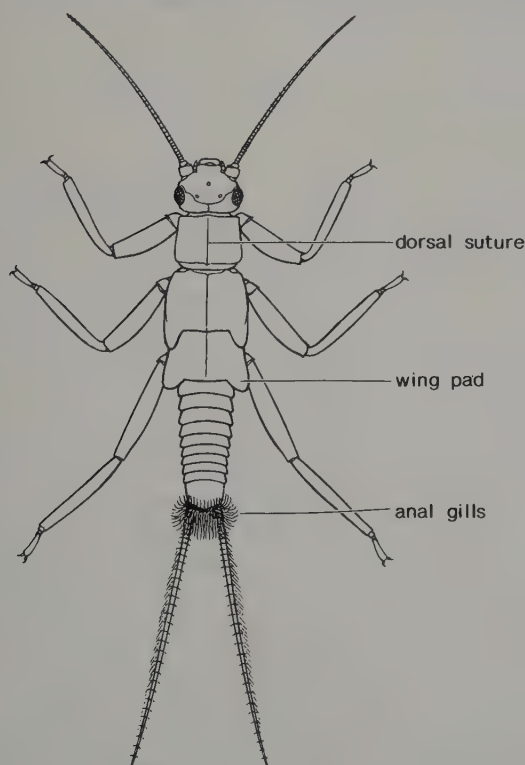


Fig. 18.3 A gripopterygid larva.

[M. Quick]

several years, depending on species, sex and environmental conditions. Northern Hemisphere stoneflies have 12–33 ecdyses; 10–14 instars are recorded in Australian Antartoperlaria. The diet of larvae varies from group to group and the mouth-parts reflect this. Australian Austroperlidae are detritivores; most Gripopterygidae are detritivore-herbivores; Eustheniidae are predominantly carnivorous and *Eunotoperla* and *Illiesoperla* are omnivorous. Larger larvae tend to be more polyphagous. A shift from one larval habitat to another is known for some species. Several terrestrial or partly terrestrial larvae are known from New Zealand and nearby subantarctic islands. Australian *Stenoperla* can live for periods in moist terrestrial habitats. Australian *Notonemoura* may wander about on damp stones at some distance from the water and *Riekoperla darlingtoni* survives drying out of its habitat, probably by burrowing. Mature larvae crawl on to rocks, logs or stems of plants at the water's edge where the adult emerges (Hynes and Hynes 1975; Hynes 1976b; Sephton and Hynes 1982, 1983; Yule 1985).

Larvae are collected by overturning rocks, and by stirring gravel in stream beds upstream from the opening of a fine meshed sieve. Some species try to avoid capture by active swimming, others by clinging to the overturned rocks.

Natural Enemies. No predators specialising on Plecoptera are known. Larvae are eaten by fish, crayfish and carnivorous larvae of Odonata, aquatic Coleoptera, Trichoptera and Plecoptera. Adults fall victim to birds, frogs, fish, bats, adult Odonata and spiders. Several parasitic organisms have been recorded as living in or associated with some extralimital species of Plecoptera: Gregarinae, Nematoda, Infusoria, fungi, Trichomycetes,

mites. The only known parasites of Australian Plecoptera are mite larvae on adults of some Austroperlidae and Gripopterygidae and trematode metacercariae in some Gripopterygidae (Hynes 1974; Zwick 1980).

Economic Significance. Stoneflies, feeding on plant tissue and being fed on in turn by other insects and fish, are a significant link in freshwater food chains. There are extralimital records of Perlidae eating eggs and hatchlings of salmonids and competing for food with trout. Stoneflies are sensitive to pollution and have been used as indicator organisms for water quality.

Special Features of the Australian Fauna

The Australian stoneflies belong to four families all of which are known only from the Southern Hemisphere. Eustheniidae, Austroperlidae and Gripopterygidae occur in Australia, New Zealand and South America, and are originally southern (Gondwanan) groups. The Notonemouridae, occurring in Australia, New Zealand, South America, South Africa and Madagascar, are a derived subgroup of a complex, exclusively northern evolutionary line. Of the 26 Australian stonefly genera 24 are endemic and two (*Stenoperla* and *Notonemoura*) are shared with New Zealand. The Australian fauna is completely endemic at the specific level. The local distribution is essentially temperate. At present 46 species are known from Tas., 75 from Vic., 91 from N.S.W., 57 from Qld (27 of these from the tropical part), seven from S.A. and four from south-western Australia. Stoneflies have not been recorded from central or north-western Australia, although there are probably some areas that would be suitable for them (Zwick 1981a; Theischinger and Cardale 1987).

CLASSIFICATION

Order PLECOPTERA (196 Australian spp.)

Suborder ANTARCTOPERLARIA (167)

- | | | |
|----------------------|-----------------------|--------------------------|
| 1. Eustheniidae (15) | 2. Austroperlidae (9) | 3. Gripopterygidae (143) |
| Diamphipnoidae (0) | | |

Suborder ARCTOPERLARIA (29)

- | | | |
|--------------------|----------------------|------------------------|
| Chloroperlidae (0) | Pteronarcyidae (0) | Leuctridae (0) |
| Perlidae (0) | Scopuridae (0) | Nemouridae (0) |
| Perlodidae (0) | Taeniopterygidae (0) | 4. Notonemouridae (29) |
| Peltoperlidae (0) | Capniidae (0) | |

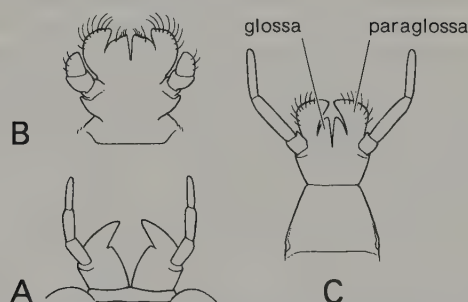


Fig. 18.4 Labia of larvae: A, *Isoperla patricia*, Arctoperlaria (after Frison 1942); B, *Illiesoperla* sp., Gripopterygidae; C, *Stenoperla* sp., Eustheniidae. [M. Quick]

Zwick's (1973, 1980) classification, based on a cladistic analysis, is adopted here. The suborders are based on primary characters of the depressor muscles of the fore leg and on a few other characters. Zwick's other supra-familial groups are Eusthenioidea (Diamphipnoidae + Eustheniidae), Gripopterygoidea (Austroperlidae + Gripopterygidae), Euholognatha (Leuctridae + Capniidae + Nemouridae + Notonemouridae + Taeniopterygidae + Scopuridae) and Systellognatha (Perlidae + Chloroperlidae + Perlodidae + Peltoperlidae + Pteronarcyidae). Alternative views are that Eusthenioidea + Systellognatha and Gripopterygoidea + Euholognatha are sister groups (Brodskiy 1982) or that the Eusthenioidea are the sister group to all other Plecoptera (C. H. Nelson 1984).

Keys to the Families of Plecoptera Known in Australia

ADULTS

1. Ano-jugal fan of hind wing with its marginal contour continuous with that of the rest of the wing (Figs 18.5A, B); abdominal segments 1–5 or 1–6 with remnants of paired lateral gills **Eustheniidae**
 Ano-jugal fan of hind wing with its marginal contour not continuous with that of the rest of the wing, forming a re-entrant angle at the end of 1A (Figs 18.5C–E, G); abdominal segments without gill remnants 2
- 2(1). Cross-veins absent from the distal half of the wings (Fig. 18.5G), rarely 1 or 2 present; cerci 1-segmented **Notonemouridae**
 Cross-veins present, generally numerous, in the distal half of the wings (Figs 18.5C–F); cerci many segmented 3
- 3(2). Generally 7 distinct veins in ano-jugal fan of hind wing and 2A branched (Fig. 18.5C); pronotum rectangular with the corners variably produced; if fewer than 7 distinct anal veins then posterior corners of pronotum very strongly produced **Austroperlidae**
 Generally no more than 6 distinct veins in ano-jugal fan of hind wing and 2A simple (Figs 18.5D, E); pronotum generally with corners not produced **Gripopterygidae**

LARVAE

1. With pairs of lateral filamentous gills on segments 1–5 or 1–6 of abdomen (Figs 18.6A, B) **Eustheniidae**
 Never with paired lateral gills on anterior abdominal segments (Figs 18.6C–F) 2
- 2(1). Without external gills (Fig. 18.6F); abdominal segments 2–9 clearly divided into tergite and sternite **Notonemouridae**
 With external anal gills (sometimes hidden under T10) (Figs 18.6C–E); last few segments of abdomen fused into complete rings 3
- 3(2). With 3 or 5 simple anal gills only, or, additionally cerci and anal plates beset with gills (Figs 18.6C, D); pronotum rectangular or with corners produced (Figs 18.6C, D); S10 absent **Austroperlidae**
 With a tuft or rosette of filiform anal gills (Fig. 18.6E); corners of pronotum generally not produced. (Fig. 18.6E); S10 generally present **Gripopterygidae**

1. Eustheniidae. Two subfamilies are recognised: Eustheniinae, confined to Chile and south-eastern Australia, and Stenoperlinae, occurring in Chile, New Zealand and eastern Australia. The large and colourful adults of Australian Eustheniidae occur in spring, summer or autumn along the banks of streams or lakes. They mostly rest in rock crevices or amongst foliage; several species are unable to fly. Adults have abundant cross-veins and remnants of lateral abdominal gills. Larvae run actively when disturbed and can swim with an undulating action.

Adults of both Australian genera of EUSTHENIINAE have a hook-like epiproct and an anteriorly extended female S9; larvae have 6 pairs of abdominal gills. In *Eusthenia* (6 spp.) the branches of Rs arise from a single stem, and all species have a large brilliant orange or purple patch over the basal portion of the hind wing. Four species are recorded from Tas., 2 from Vic. and south-eastern N.S.W. One mainland species apparently is confined to the Otways in Vic.; the other, which is unable to fly, is more widely distributed in mountainous Vic. and N.S.W. with a brachypterous population on Mt Kosciusko. *Thaumato-perla* (4 spp.) has several branches of Rs arising separately from R₁, and very short and broad wings; none of the species is able to fly. All have mainly dark to almost black wings, but the body may have bright markings. The species occur allopatrically on high mountains of Vic., differ significantly in colours and slightly in size, but lack striking structural differences.

The only Australian genus of STENOPERLINAE, *Stenoperla* (5 spp.), ranges from Cape York Peninsula to southern Vic. There are 2 species in New Zealand. The male epiproct is not hook-shaped and S9 of the female is

not extended anteriorly; the body is long and slender and the wings are generally long and relatively narrow. All species can fly. Their hind wings may be vivid green, pink or purple or more inconspicuously reddish to greyish brown. Larvae have only 5 pairs of lateral abdominal gills. Two distinct species groups of Australian *Stenoperla* have been distinguished. Three or 4 species coexist in some areas of north-eastern N.S.W. Larvae have been found from sea-level up to 1800 m. [Theischinger and Cardale 1987]

2. Austroperlidae. This is a small family confined to Australia, New Zealand and South America. Adults of Australian species are of medium size (body 8–28 mm, fore wing 4–24 mm) and characterised by a pronotum with sharp or produced corners. Larvae have a similar pronotum, live in streams under stones or in gravel and are often associated with organic debris or logs.

Austroheptura (3 spp.), *Austropentura* (2 spp.) and *Tasmanoperla* (2 spp.) are very closely related to each other and to *Austroperla* from New Zealand. They are either brown and yellow in strong contrast or more uniformly brown, and in most species there is a pale patch on the otherwise dark, mottled fore wings; some species are often or exclusively brachypterous. Larvae of *Austroheptura* and *Tasmanoperla* have 7 beaded anal filaments, those of *Austropentura* 5. Two species of *Austroheptura* and one of *Austropentura* occur in south-eastern N.S.W. and Vic., one *Austropentura* and both *Tasmanoperla* are confined to Tas., and one *Austroheptura* ranges from north-eastern N.S.W. into south-eastern Qld.

Acruroperla (1 sp.; south-eastern N.S.W. and Vic.) is spectacular, having a metallic blue or black body and dark wings with red or yellow costal margins. The body and

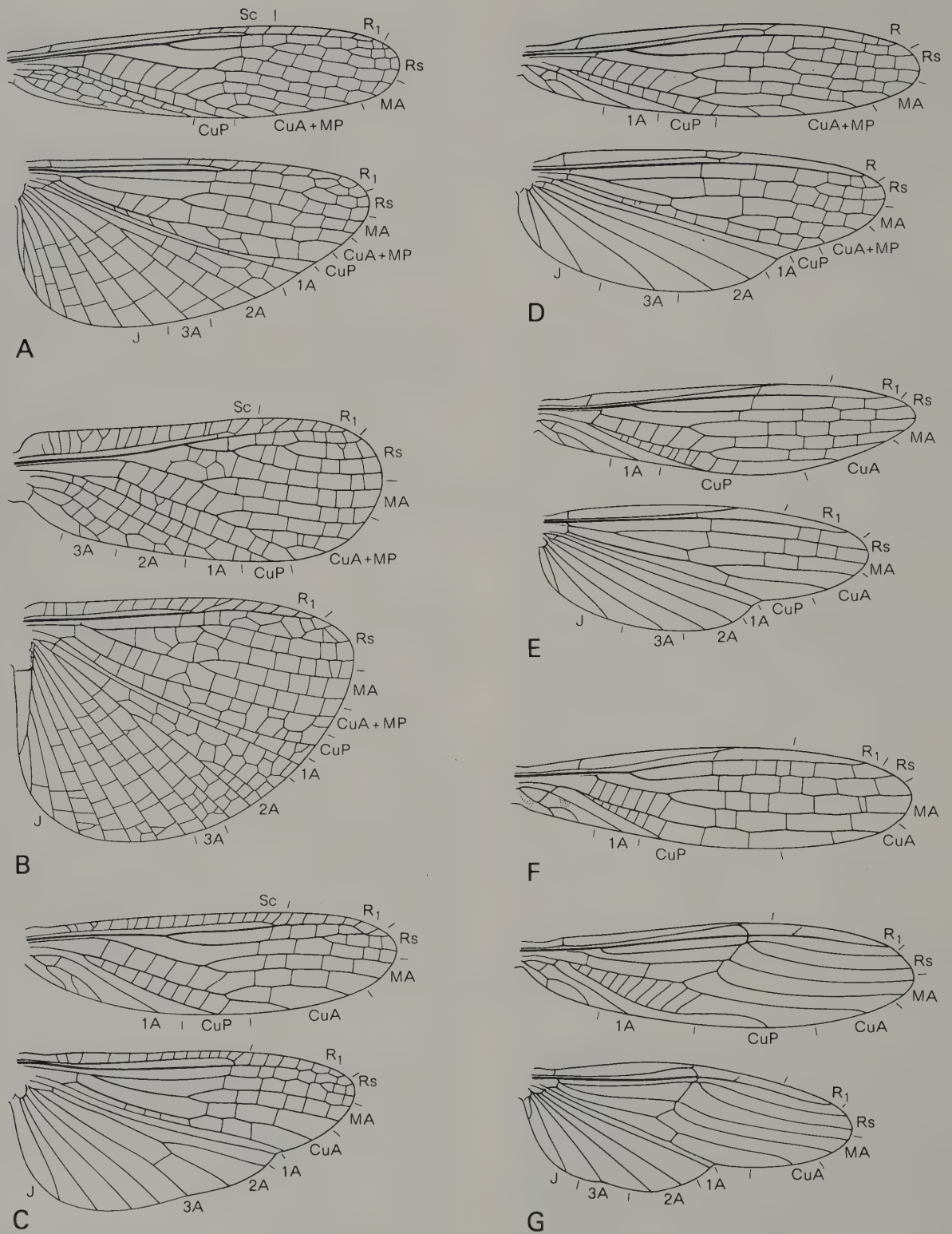


Fig. 18.5 Wings: A, *Stenoperla*, Eustheniidae; B, *Eusthenia*, Eustheniidae; C, *Acruroperla*, Austroperlidae; D, *Illiesoperla*, Gripopterygidae; E, *Dinotoperla*, Gripopterygidae; F, *Riekoperla*, Gripopterygidae; G, ?*Austrocerca*, Notonemouridae.

[M. Quick]

wings of *Crypturoperla* (1 sp.; Tas.) are uniformly dark. Larvae of both genera have conspicuous paired abdominal tubercles (Fig. 18.6C). Larvae of *Crypturoperla* occur in cold, steep, high altitude streams, usually associated with moss on rock faces. [Theischinger and Cardale 1987]

3. Gripopterygidae. These are the dominant stoneflies in Australia and occur also in New Zealand (including

Auckland and Campbell Is) and in South America. Most adults are dull coloured, with wings either uniformly infusate, darkened or brightened at the cross-veins, banded or mottled. Larvae generally range from yellow to dark greyish brown in colour and have a bunch of cylindrical anal gills between the bases of the usually long cerci; one South American genus (*Notoperla*) lacks gills. They are rather sluggish and are usually found clinging to

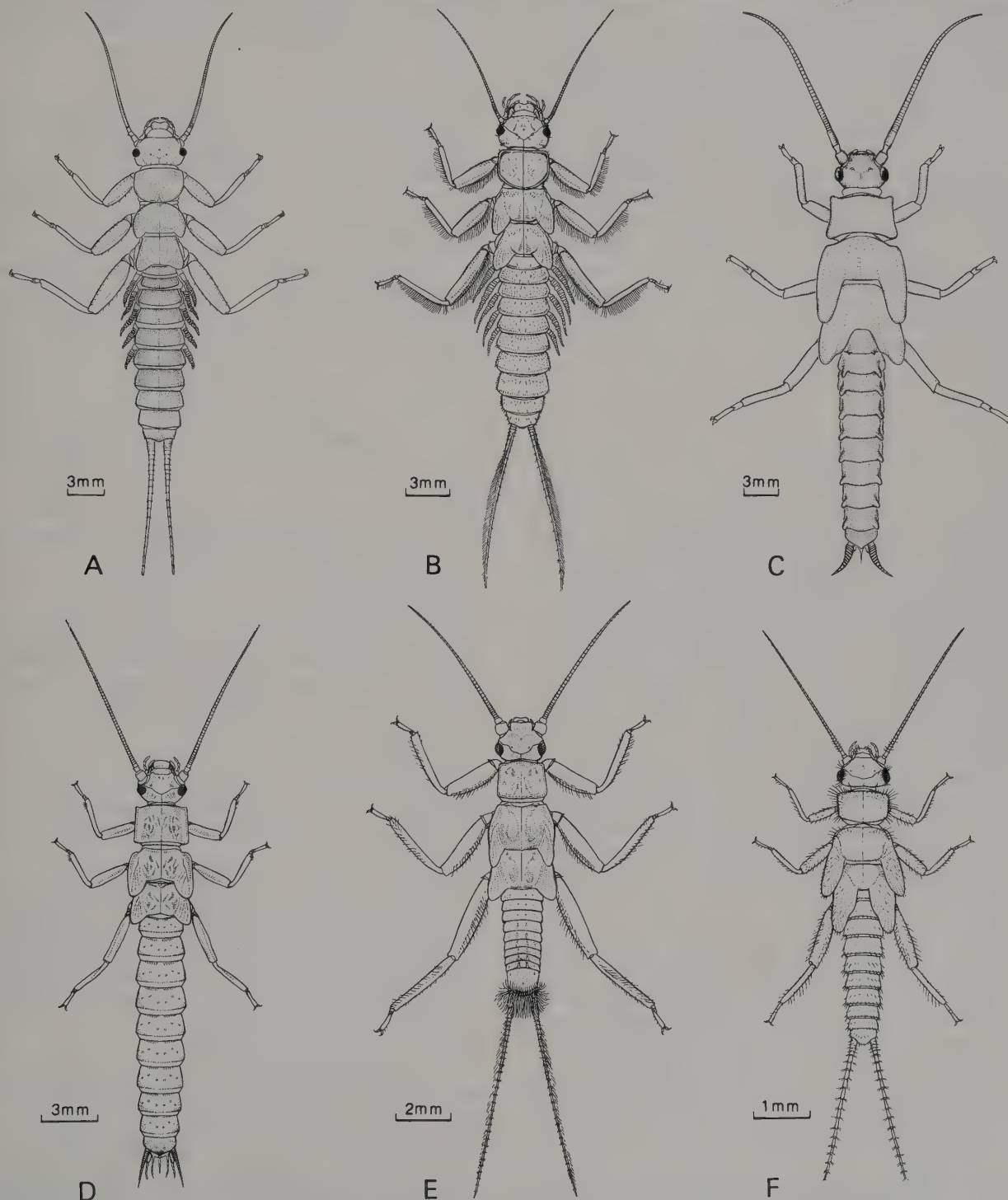


Fig. 18.6 Larvae: A, *Stenoperla denise*, Eustheniidae; B, *Stenoperla kuna*, Eustheniidae; C, *Acruroperla*, Austroperlidae; D, *Tasmanoperla*, Austroperlidae; E, *Illiesoperla*, Gripopterygidae; F, ?*Austrocercella*, Notonemouridae. [A, C by S. Smith; B, D, E, F by M. Quick]

the undersurface of rocks and debris in swift water. There are 12 Australian genera.

Eunotoperla (1 sp.), with cross-veins between CuP and 1A of the fore wing is as large as some Eustheniidae (body 20–25 mm, fore wing 10–30 mm). Populations from different localities may vary greatly in wing length. Larvae, with spines on the trochanters and femoral processes, occur in small, shaded, stony streams of south-eastern N.S.W. and Vic.

Illiesoperla (12 spp.) and *Trinotoperla* (17 spp.) are mostly of medium size (body 8–22 mm; fore wing 8–25 mm), with Rs and CuA of the fore wing forked and the cerci short. The hind margin of the metabasisternum is V-shaped in *Illiesoperla*, almost straight in *Trinotoperla*. Larvae of *Illiesoperla* are similar to *Eunotoperla*, but have a flap-like frons almost covering the clypeus and lack femoral processes. Larvae of *Trinotoperla* have long antennae and cerci and are recognised readily by their sprawling habit with long legs spread sideways. Some *Trinotoperla* are adapted to steep rock faces of waterfalls and seepages, some *Illiesoperla* to slow-flowing and rather warm streams. *Illiesoperla* ranges from Cape York to King I.; *Trinotoperla* from Cape York Peninsula to Tas. Several species of each genus may coexist in the same streams.

Dinotoperla (35 spp.), *Dundundra* (1 sp.), *Neboissoperla* (3 sp.) and *Nescioperla* (1 sp.) are generally smaller (body 4.5–12 mm, fore wing 1–16 mm), with Rs simple and CuA forked in the fore wing, and the cerci short. Larvae of *Neboissoperla* are very similar to some *Trinotoperla*; larvae of *Dinotoperla* have either very short or very thin and attenuated cerci; larvae of *Dundundra* and *Nescioperla* are unknown. *Dinotoperla* larvae can be found in almost any type of stream, some even in intermittent streams and stagnant pools, whereas *Neboissoperla* apparently favours cool conditions. *Dinotoperla* ranges from Cape York Peninsula to south-western Australia, usually with several sympatric species. *Neboissoperla* has one species in mainland, alpine regions, one in Tas. (known from larvae only) and one from montane north-eastern N.S.W. Adults of *Dundundra*, with very wide hind wings with unique venation, occur on the Lamington Plateau in south-eastern Qld in autumn. *Nescioperla*, with fewer cross-veins in the fore wing than related genera, is confined to Iron Range on Cape York Peninsula.

Adults of *Cardioperla* (10 spp.), *Kirrama* (1 sp.), *Leptoperla* (30 spp.), *Newmanoperla* (5 spp.) and *Riekoperla* (27 spp.) are mostly small (body 5–15 mm, fore wing 0–14 mm), with Rs and CuA of the fore wing simple and the cerci long. Larvae of *Leptoperla* are generally long-legged and slender, those of *Cardioperla* and *Riekoperla* have a small, transverse sclerite above the gills and below T10 and are uniformly coloured, whereas at least some *Newmanoperla* are remarkably patterned; *Riekoperla* larvae may be dorsally flat or have huge dorsal hooks. The larva of *Kirrama* is unknown. Some *Leptoperla* inhabit slow streams, lakes or swamps; some *Cardioperla*, *Leptoperla* and *Riekoperla* represent a mountain-top 'trickle fauna', some *Riekoperla* are known

mainly from swamps. Both *Leptoperla* and *Riekoperla* have one species each in W.A. and S.A., very few in Tas. and numerous species in eastern mainland Australia. *Leptoperla* extends to Cape York Peninsula, *Riekoperla* into south-eastern Qld. *Newmanoperla* has one species each in north-eastern Qld, Tas. and W.A. and 2 in south-eastern mainland Australia. *Cardioperla* is confined to Tas. and *Kirrama* to tropical Qld. A pale wingless *Leptoperla* is known from the summit of Mt Kosciuszko and an almost wingless, exceptionally large *Riekoperla* from Mt Donna Buang in Vic. [Theischinger and Cardale 1987]

4. Notonemouridae. The family occurs also in South America, South Africa, Madagascar and New Zealand. Adults differ from other Australian stoneflies in lacking cross-veins in the distal portion of the wings (Fig. 18.5G), larvae by the lack of external gills and by their abdominal segments 2–9 being clearly divided into tergite and sternite. Different specialisations in the male and female genitalia define two groups of genera. Australian members of the *Aphanicerca* group (*Austrocerca*, *Austrocercella*, *Austrocercoides*, *Kimminsoperla* and *Tasmanocerca*) have only simple anal veins in the hind wing, whereas the only member of the *Notonemoura* group in Australia, *Notonemoura* (which also occurs in New Zealand), has 2A forked. Larvae of most Australian genera are very similar, slim and without significantly enlarged legs. Larvae of *Notonemoura* are very stocky with large hind femora.

Males of *Austrocerca* (2 spp.) have a plump subgenital plate and minute paraprocts. One species is known from south-eastern Australia, the other from Tas. only.

Males of *Austrocercella* (15 spp.) have an elongate subgenital plate with subapical paraprocts. Known from south-eastern Qld to Tas. but with greatest diversity (8 spp.) in the alpine region. Several species often coexist in the same streams and apparently emerge in a seasonal sequence. Larvae are found in gritty silty gravel where they possibly burrow.

Austrocercoides (3 spp.), is confined to the south-eastern mainland and Tas. Males have 3 apical lobes on the subgenital plate. Larvae are always associated with silty embayments where they are often common in wood debris.

Males of *Kimminsoperla* (6 spp.) have a long subgenital plate and paraprocts inserted basally on S10. There are 3 species in Tas. and 3 from eastern N.S.W., one of them extending into south-eastern Qld. One of the mainland species is apparently coastal, the second more montane and the third possibly confined to the Nandewar Range in north-eastern N.S.W. Larvae seem to be associated with areas of quiet flow over sandy gravel.

Tasmanocerca from western Tas. (1 sp.) has 2 transverse pale fasciae on otherwise dark fore wings. Larvae inhabit stony trickles, streams and rivers in forest.

The larger of the Australian species of *Notonemoura* (2 spp.) is known from south-eastern Qld, north-eastern N.S.W. and Vic., the smaller from Vic. and Tas. Strangely, Qld populations of the larger species and Tasmanian populations of the smaller species have conspicuously spotted

wings, whereas the wings of populations of both species from elsewhere are rather unicolorous. Adults have strong hind legs and jump away if disturbed. Larvae live in thin films of water, particularly on vertical rock faces. The larger species inhabits swift to medium-swift rocky streams in forest, the smaller tiny trickles at high altitude in fern gullies. [Theischinger and Cardale 1987]

ACKNOWLEDGMENTS. The opportunity to make use of the information in Riek (1970, 1974a), is gratefully acknowledged. I am also indebted to Prof. Dr H. B. N. Hynes (Waterloo, Canada) and to Prof. P. Zwick (Schlitz, Federal Republic of Germany) for valuable comments and criticisms on a draft of this chapter.

Blattodea

Blattaria

(*Cockroaches*)

L. M. ROTH

Exopterygote Neoptera; body flattened dorsoventrally; head in repose with chewing mouth-parts directed downwards. Fore wings, when present, usually modified into hardened tegmina which are sometimes abbreviated or absent; hind wings, if developed, membranous, but these too may be reduced or absent. Legs cursorial, sometimes fossorial; tarsi 5-segmented. Male genitalia asymmetrical, female ovipositor concealed. Cerci with 1 to many segments. Specialised stridulatory organs rarely present. Eggs usually contained in an ootheca which may be carried externally until hatching or deposited on a substrate (oviparity), or retracted into a uterus or brood sac until parturition (ovoviviparity and viviparity).

Cockroaches are primitive orthopteroids and among extant orders have been grouped with Mantodea, Isoptera, Grylloblattodea, Orthoptera, Phasmatodea, Dermaptera, Embioptera, Plecoptera and Zoraptera, all groups which retain primitive features of the Neoptera (Brown 1982). McKittrick (1965) and others believe they are most closely related to termites. Although the Blattodea is presently relatively small, containing fewer than 4000 named species and about 460 genera, during the late Palaeozoic era (Carboniferous), it was one of the largest of insect orders in numbers of individuals (Carpenter 1980).

There is considerable variation in the size of Blattodea, not only between species, but intraspecifically as well. In Australia the smallest and most fragile species belong to *Nocticola* which are about 3 mm long and weakly sclerotised. The largest species belong to the Blaberidae, particularly the Panesthiinae. The wingless *Macropanesthia rhinoceros* may attain a length of 65 mm and weigh about 20 grams (Day 1950) probably making it the bulkiest cockroach known.

The biology of cockroaches has been reviewed by Cornwell (1968), Guthrie and Tindall (1968), Beier (1974) and Bell and Adiyodi (1981). Schal *et al.* (1984) summarised the behavioural ecology of cockroaches and

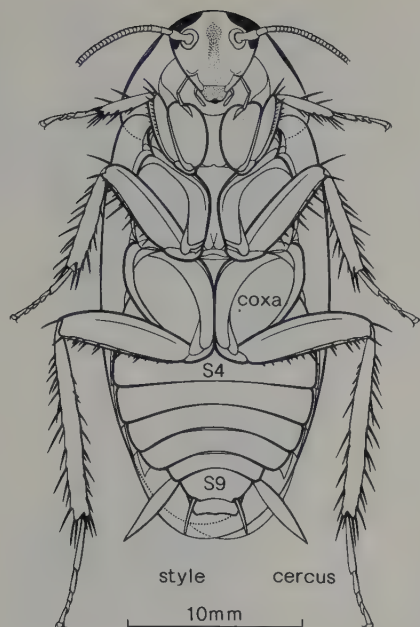
Roth and Willis (1957, 1960) reviewed their medical and veterinary importance, and biotic associations. Princis (1962–71) compiled the biological and taxonomic literature.

Anatomy of Adult

Head (Fig. 19.2A). Hypognathous, with most of the sclerites well defined. Compound eyes nearly always developed, but may be reduced or absent (especially in cavernicolous forms); lateral ocelli usually represented by 2 pale ocelliform spots. Antennae many segmented, filiform. Mandibles strong and toothed; maxillary palps 5-segmented; labial palps 3-segmented.

Thorax. Prothorax with a large, shield-like pronotum, sometimes overlapping the head. Meso- and metanotum more or less rectangular and similar to each other. Pleura and sterna weakly sclerotised, somewhat compressed, mostly hidden by coxae; meso- and metathoracic spiracles present.

Legs (Figs 19.1, 2B). Coxae closely approximated, very wide, often flanged; tarsi 5-segmented (fewer tarsomeres result from regeneration if the leg is lost or damaged during the nymphal stage); tarsomeres 1–4 usually with pulvilli; terminal segment always with claws, with or without

Fig. 19.1 *Methana marginalis*, ♂, ventral.

[F. Nanninga]

an arolium; pulvilli and arolia often are reduced or absent in cavernicolous forms, but these structures also may be absent in epigeic forms. The types of spines on the anteroventral margin of the fore femur are important taxonomically.

Wings (Fig. 19.2c). The tegmina of species with fully developed flight organs, usually are more or less sclerotised, and protect the membranous hind wings. Costa (C) of tegmen marginal, Sc short and Rs usually with many anterior pectinate branches; MA and CuA occupy a large part of the tegmen, and the short, curved CuP cuts off a distinctly shaped clavus. Hind wing usually with a large anal lobe folded at rest between CuP and 1A, and usually further folded in a fan-like manner.

The venation of the hind wing is important taxonomically, particularly whether the cubitus is branched or not, and if branched, the number of rami and whether they are complete (i.e. reach the apical margin), or incomplete (do not reach apical margin) (Fig. 19.9). A species may have both brachypterous and macropterous morphs. Some taxonomists have placed too much emphasis on reduction of flight organs and have used it as a principal generic or specific character.

Abdomen (Figs 19.5–7). Ten terga (T1–T10), the 11th absorbed into T10 (supra-anal plate). First sternum small or absent, the 11th represented by the paraprocts which are concealed by the subgenital plate ventrally. Spiracles of segments 2–7 open on the pleural membrane, those of 1 and 8 are attached to the lateral margins of the terga.

The male subgenital plate (S9) usually bears a pair of styles (Fig. 19.1), and these may be specifically distinctive. In Australian taxa the males of *Ectoneura*, *Stenectoneura*, and *Richanitschia luteomarginata* (Blattellidae) have a single style. Styles are absent in males of all Panesthiinae (Blaberidae) (Roth 1977). Outside Australia (mostly from Asia and Africa) there are about

10 blattellid genera whose males lack styles (Roth 1989). Some species, including *Shelfordina orchidae*, recently reported from Australia (Rentz 1987c), and at least 3 other undescribed species of the genus, have a process arising near the base of each style giving the appearance of 4 styles (Roth 1990b).

The male genitalia, consisting of a group of asymmetrical, sclerotised phallomeres, are concealed in the genital pouch and often show excellent specific characters. The phallomeres are complex in the Blattidae (Fig. 19.3c) and Polyphagidae, and are simpler in the Blattellidae and Blaberidae (McKittrick 1964). Mizukubo and Hirashima (1987) and Bohn (1987) have studied the homologies of the male genital sclerites.

In the female, the subgenital plate, formed by S7 and S8 is inflected and, with S9, is absorbed into the wall of a large genital atrium (Fig. 19.3A). The ovipositor consists of 3 pairs of small, finger-like valves inside the chamber (Fig. 19.3B).

Sexual Dimorphism. In at least 3 genera of Australian cockroaches sexual dimorphism is so marked that males and females appear to belong to different taxa. The tegmina of females of *Escala* and *Robshelfordia* (Blattellidae) are reduced to lateral pads and the hind wings are absent. In the blaberid *Laxta granicollis* (Figs 19.11B, C), the

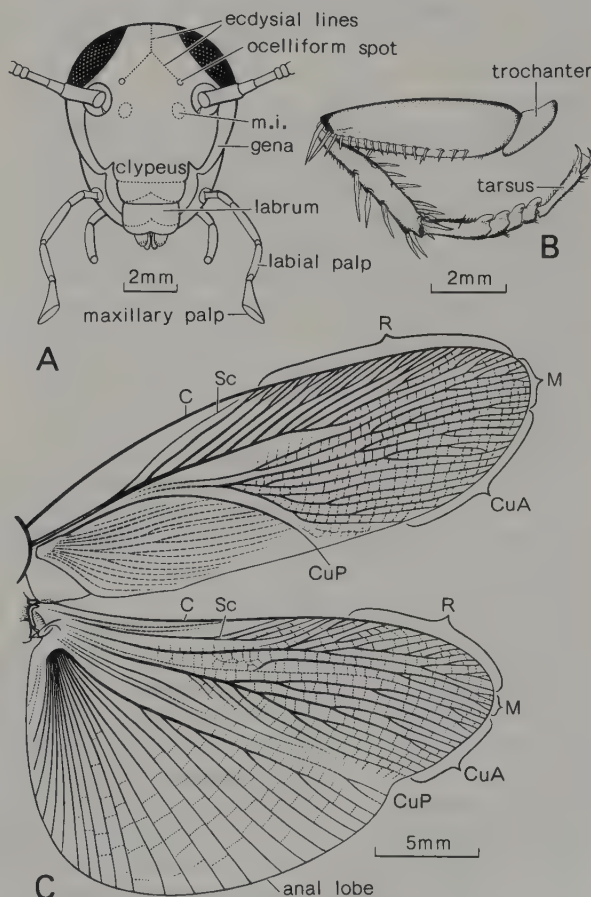


Fig. 19.2 A, *Polyzosteria limbata*, head, frontal semidiagrammatic (m.i., impression of transverse frontal muscle); B, *Periplaneta brunnea*, fore leg; C, *P. brunnea*, right tegmen and hind wing.

[F. Nanninga]

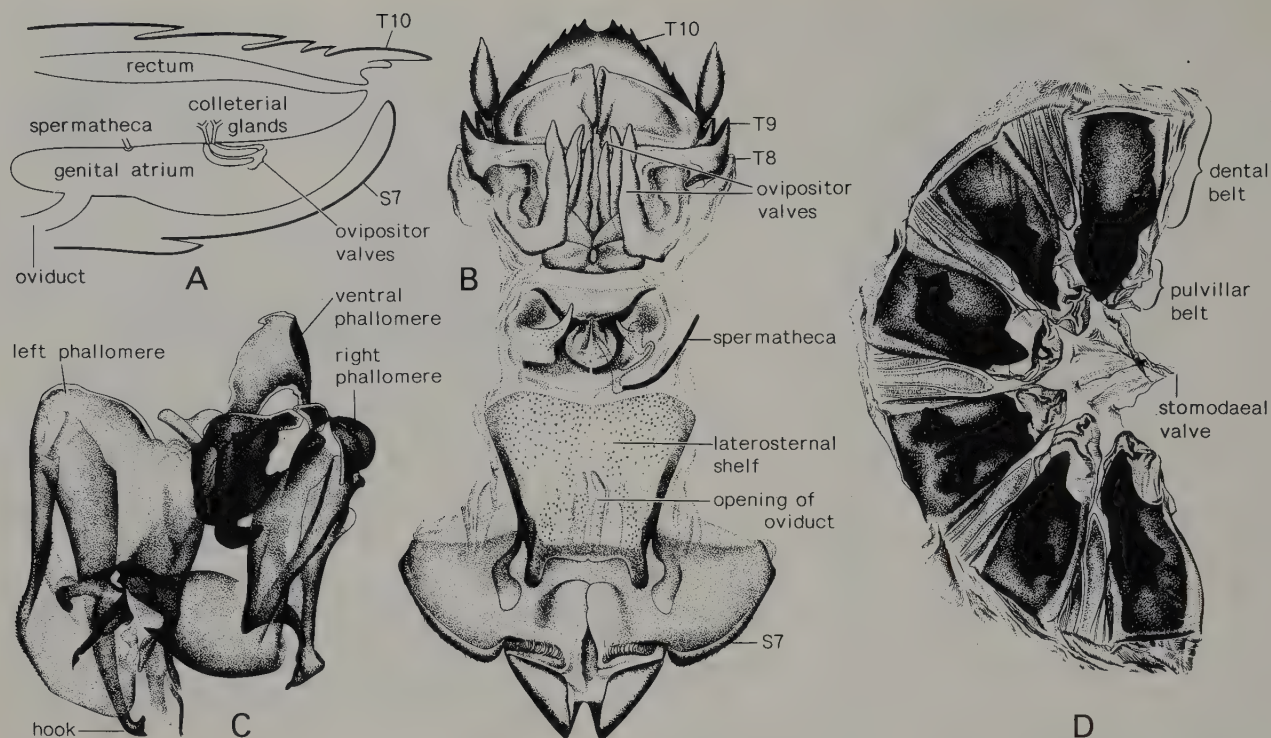


Fig. 19.3 A, ♀ genital atrium, median sagittal section, diagrammatic; B, *Platyzosteria melanaria*, ♀ genital atrium (the lateral walls have been cut and the roof reflected upwards); C, *Polyzosteria viridissima*, ♂ (ventral phallomere reflected anteriorly); D, *Polyzosteria limbata*, proventriculus (slit longitudinally). [F. Nanninga]

females are apterous. The males in these 3 genera have completely developed tegmina and wings. However, in most species of cockroaches adult males superficially resemble females, but can be distinguished by the presence of styles and tergal glands (when present), small subgenital plate (Figs 19.1, 19.5–7B) and genitalia (Fig. 19.3C; seen by preparing a slide or separating the supra-anal and subgenital plates). Adult females always lack styles and tergal glands, have a larger subgenital plate (Figs 19.5–7C), and their ovipositor valves (Fig. 19.3B) readily distinguish them from males.

Internal Anatomy. Crop well developed, proventriculus provided with large or medium sized denticles (Fig. 19.3D), except in the Blaberidae in which they are very small; mid gut with 8 caeca and about 80–100 Malpighian tubules arranged in groups of 6 (Blattidae), 4 (Blattellidae) or 3 (Blaberidae) (Leconte *et al.* 1967).

Cockroaches have a variety of abdominal glands that are used in defence (Figs 19.5B, C), or in sexual behaviour (Fig. 19.6A) (Roth 1969; Roth and Alsop 1978; Brossut and Roth 1977). Tergal glands involved in sexual behaviour occur only in males and their presence or absence, and location, are taxonomically important. A genus may contain species that have or lack visible tergal glands, and they may occur on different abdominal terga. There are a pair of ovaries each consisting of panoistic ovarioles whose number of oocytes determines the number of eggs which will be deposited. The number of yolk-filled oocytes at the time of ovulation varies and shows family differences (Roth 1968a). Paired colleterial glands

(Fig. 19.3A) secrete a proteinaceous material and a diphenolic compound which form a quinonoid tanning agent during the formation of the ootheca (Stay and Roth 1962).

Immature Stages

Eggs and Oothecae. With the exception of 4 genera of Panesthiinae, all cockroaches that have been studied produce an ootheca or egg case. In oviparous species, the newly formed ootheca is pale and soft, but hardens when exposed to air. The dorsal ovipositor valves serve as a mould and impart characteristic and sometimes diagnostic shapes to the keel. Each egg lies in a cell surrounded by an air space with a duct in the keel leading to external air. The keel usually is serrated, the number of teeth often corresponding to or approximating the number of eggs present. Oothecae of different species may be distinctive (Roth 1968b, 1971), differing in size, shape, surface ornamentation, shape of keel serrations and number of contained eggs. Ovoviviparous species of Blaberidae generally have a larger number of eggs per ootheca, but produce fewer egg cases than oviparous species. The number of eggs per ootheca in Australian species ranges from 12 to 40 (P. Pope 1953).

Nymphs (Figs 19.4B–D). Immature cockroaches resemble adults in general structure but lack tegmina and wings, and often differ in colour and texture. All early instars resemble males in having S8 and S9 visible, and bear styles on S9. In females, the styles disappear in later stages. In alate species the wing buds appear late in development. The number of moults varies between taxa and

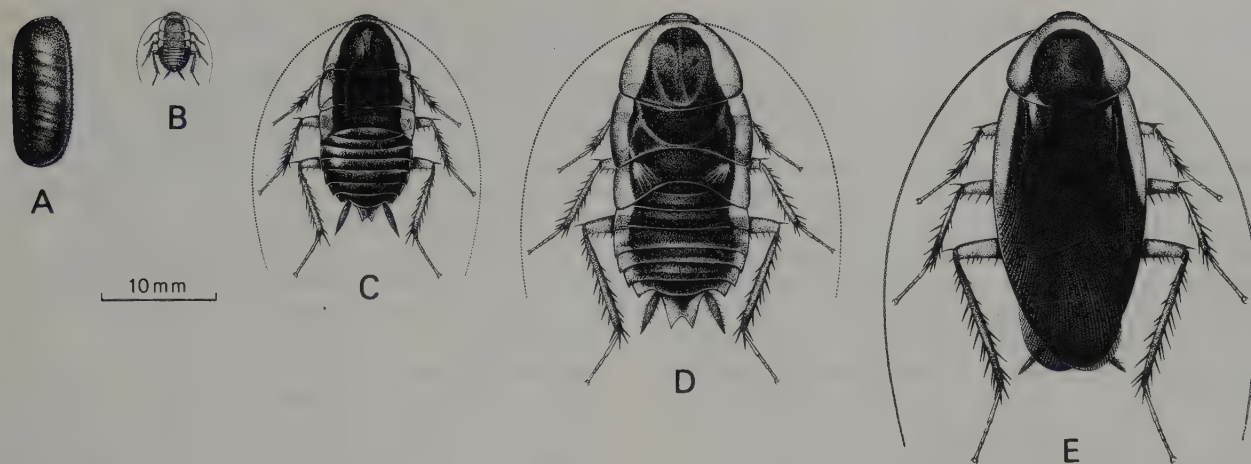


Fig. 19.4 *Methana marginalis*, stages of development: A, ootheca; B, young nymph; C, medium-sized nymph; D, large nymph; E, adult.

[F. Nanninga]

sometimes differs between sexes of the same species (Willis *et al.* 1958). Early instars, where both sexes have styles, can be sexed by differences in shape of S9 (Ross and Cochran 1960; Lawson and Lawson 1965).

Biology

Habitats. The varied habitats of cockroaches were reviewed by Roth and Willis (1960). Most cockroaches are nocturnal, usually are found near the ground, and hide under bark, logs or stones during the day. Some diurnal species like *Ellipsidion* (Figs 19.8H, I), are arboreal and run amongst foliage in bright sunlight. *Polyzosteria viridissima* (Plate 2, B), also a diurnal species, is conspicuous in the mountainous regions of eastern Australia, where it perches on low bushes, and *Polyzosteria limbata* also basks in the sun on bright days. Several species of *Polyzosteria* and *Euzosteria* are adapted to arid conditions. Numerous species of *Balta*, and others, are found in tropical forests from sea level to about 1800 m. A. M. Richards (1967) recorded 10 species of cockroaches from caves. The troglobitic blattellid, *Trogloblattella nullarborensis* (Fig. 3.6) is blind and occurs in limestone caves in the Nullarbor Plain (M. J. Mackerras 1967c); *T. chapmani*, the only other species in the genus, occurs in limestone caves in Sarawak (Roth 1980). *Shawella atra* and *Shawella douglasi* are found in mines or caves in W.A. (Princis 1963). A nocticolid, *Nocticola australiensis*, occurs in the Chillagoe Caves, Qld (Roth 1988). Other Australian cavernicolous species differ in showing little or no modifications for life in caves. The winged males of some species, especially *Calolampra* (Fig. 19.11D), and *Balta*, are attracted to light. Some Panesthiinae live in and eat rotting wood, or burrow in the soil and feed on surface detritus, but the food of most native species is unknown. Amphibious species of Epilamprinae (Blaberidae) occur in Central America, Burma, Thailand, Japan and India, but none have been recorded from Australia. However, there are 3 Australian species of *Rhabdoblatta*, and many semiaquatic species of this genus are found near streams.

Reproduction. Mating is almost invariably preceded by courtship involving male and female pheromones.

Secretions from male tergal glands serve to manoeuvre the female into the precopulatory position and arrest her movement while she feeds on or palpates his dorsum, especially in the glandular area. This stimulates him to push backwards, grasp her genitalia, and swing about so that the pair are joined end to end, their heads facing in opposite directions (Roth and Willis 1952, 1954). Copulating pairs (Fig. 1.27B) remain joined for some time during which a spermatophore is formed and transferred to the female's atrium or bursa copulatrix. Males of most species of Blattellidae have uricose accessory glands which store uric acid; after the spermatophore is inserted, uric acid flows over it and hardens (Roth and Dateo 1965; Roth 1967a). The empty spermatophore and attached uric acid is dropped after a day or two. Females of *Blattella germanica* eat the uric acid after it is dropped (Mullins and Keil 1980), whereas those of *Xestoblatta hamata* eat it while it is still attached to her (Schal and Bell 1982). These species incorporate the uric acid nitrogen into their oothecae.

There are 4 types of reproduction:

1. OVIPARITY (all families except Blaberidae). A hardened ootheca is carried for various lengths of time before being deposited on a substrate; however, all species of *Blattella* carry the ootheca externally for the entire embryogenetic period. During embryogenesis only water is taken up by the eggs from the substrate, or from the mother.

2. FALSE OVOVIVIPARITY (almost all Blaberidae, and 2 genera of Blattellidae). When the ootheca is completely extruded, it is retracted into a uterus or brood sac where the eggs develop (e.g. species of *Calolampra*, *Laxta*, *Panesthia*). The oothecal membrane is greatly reduced. In *Stayella* the ootheca is practically identical to those of *Blattella* spp., but it is retracted completely into the abdomen (Roth 1982b, 1984). When first laid, eggs of false ovoviparous taxa have enough yolk to complete development and take up only water from the mother.

3. TRUE OVOVIVIPARITY (the panesthiine blaberid genera *Macropanesthia*, *Geoscapheus*, *Neogeoscapheus* and *Parapanesthia*). This differs from false ovoviviparity in

that an ootheca is not formed. Eggs pass directly from the oviduct into the uterus where they lie in a jumbled mass (Rugg and Rose 1984a).

4. **VIVIPARITY** (known only in the blaberid *Diploptera punctata* but probably other species of the genus are viviparous also). The oothecal membrane is very incomplete. The eggs are very small when laid and lack sufficient water and yolk to complete development. Nutrients and water are obtained from the mother during embryogenesis (Roth 1967b). The embryos drink water and dissolved proteins and carbohydrates synthesized and transported by the uterus during gestation (Ingram *et al.* 1977).

During the evolution of ovoviviparity and viviparity in the Blaberoidea, the ootheca changed from a hard rigid structure, completely enclosing the eggs and deposited relatively shortly after its formation, to a soft, flexible, transparent membrane, often incompletely enclosing the eggs, that was retracted and incubated internally (Roth 1968b). Finally there is a complete loss of the membrane, an ootheca is not formed, and the eggs pass directly into the uterus (Rugg and Rose 1984a).

When the ootheca is formed, the eggs are arranged vertically with their micropylar ends facing dorsally. Some oviparous species deposit their oothecae without first changing its vertical position (e.g. Blattidae, Figs 19.4A, 8A), whereas others rotate the egg case 90° shortly after its formation (Fig. 19.8r), and then deposit it (e.g. Blattellidae: Blattellinae), or carry it externally (*Blattella* spp.). Ovoviviparous species retract the ootheca (e.g. the blattellid *Stayella*, most Blaberidae) (McKittrick 1964; Roth 1967d, 1968b, 1971, 1982b, 1984). The brain is not required for oviposition in the Blaberidae where the control centre for formation, 90° rotation, and retraction of the ootheca lies in the abdomen and last abdominal ganglion. In *Periplaneta americana* the brain is needed for initiating ootheca formation but is unnecessary once the process has begun (Roth 1974a).

Oviparous species differ in the manner of depositing their oothecae. In captivity some simply drop them, others glue them to bark (e.g. *Ellipsidion* spp.), and some glue them to the substrate and cover them with foreign material (e.g. *Methana marginalis* and *Polyzosteria limbata*). McKittrick (1964) described some of the procedures employed by females to conceal their oothecae.

In oviparous species, hatching of eggs requires a group effort on the part of all the embryos in an egg case. They swallow air, become inflated, force the separation of the two halves of the keel, and escape more or less simultaneously (Roth and Willis 1958, pl. 26; Provine 1982). At parturition in ovoviviparous and viviparous species, the ootheca is extruded, and the nymphs, which also swallow air at that time, are freed from the confines of the abdomen, still enclosed in their embryonic cuticle which they shed quickly.

Pycnoscelus surinamensis is the only cockroach known to reproduce by obligatory parthenogenesis; usually only females are produced but parthenogenetically produced, non-functional males occur occasionally. The species has become established in Europe, North America, South America and Australia (Roth and Willis 1961).

Pycnoscelus indicus, the sibling species from which the parthenogenetic taxon undoubtedly arose, can only reproduce bisexually (Roth 1967c). Both species are polymorphic with regard to chromosome number, and some clones of *P. surinamensis* probably arose polyphyletically by polyploidy and/or aneuploidy (Roth and Cohen 1968). The biotic potential of different clones of *P. surinamensis* varies, but generally is lower than that of *P. indicus* (Roth 1974b). *Periplaneta americana*, *Blatta orientalis*, *Nauphoeta cinerea*, *Blattella germanica* and *Supella longipalpa* all exhibit some degree of parthenogenesis (Roth and Willis 1956).

Natural Enemies and Defence. The oothecae of *Ellipsidion*, which are frequently deposited in exposed places, often serve as hosts for hymenopterous egg-parasites. Ground-dwelling cockroaches are parasitized by several species of parasitic Rhipiphoridae (Coleoptera) and there is a correlation between host family and parasite genus (Riek 1955a). Cockroaches are preyed upon by many terrestrial arthropods, as well as by frogs, reptiles and insectivorous birds and mammals (Roth and Willis 1960).

Cockroaches can escape capture by the use of defensive secretions (Roth and Alsop 1978), through evasive behaviour, concealment, protective coloration and mimicry. Most of the Polyzosteriinae (Blattidae) produce aliphatic compounds, most often *trans*-2-hexenal, for defence against predators (Waterhouse and Wallbank 1967; Wallbank and Waterhouse 1970). Some *Platyzoisteria* assume a characteristic warning stance in which the head is held near or touching the ground, and the abdomen is flexed upwards at a sharp angle, revealing bright orange-yellow markings on their coxae and venters. The gland opening is pointed towards the disturbance and continued irritation results in the discharge of a secretion which is principally 2-methylenebutanal. When disturbed, *Diploptera punctata* expels a mixture of quinones from the second abdominal trachea (Roth and Stay 1958).

Females of *Perisphaerus* (Blaberidae) can roll themselves up into a spherical ball when alarmed, and because of their convex form and shiny black colour closely resemble pill-millipedes. When rolled up, all of their vulnerable structures are completely hidden and protected, and they are invulnerable from ant attack. Very young nymphs cling to the undersurface of their mothers, and are also protected when the mother is in the ball position. The males are fully winged and do not assume this protective stance (Roth 1981).

Parasites. There are many protozoan and helminth parasites of cockroaches (Roth and Willis 1960), but few have been reported from Australia. Large species of amoebae, ciliates belonging to the Clevelandellidae, and nematodes occur in the hind gut of *Macropanesthia rhinoceros* (Day 1950). Gordiid worms (Nematomorpha) may occur in the body cavity. The oxyurid nematode, *Blattophila sphaerolima* is found in *Panesthia laevicollis*.

Economic and Medical Significance. Less than 1% of the described species are domiciliary pests. Most cockroaches prefer a tropical climate, but can withstand short

exposure to extreme cold. They destroy foodstuffs by eating them and their excreta foul whatever they walk on. They will eat labels off containers and the bindings of books. They are abundant in earth closets, and congregate in countless numbers in sewers in warmer parts of the country. Ten cosmopolitan species have been introduced into Australia where they are pests in dwellings, markets, storehouses, etc. *Blatta orientalis* is present in the southern part of the continent. *Periplaneta americana* and *P. australasiae* are widespread, troublesome insects. *Periplaneta fuliginosa*, reported from Melbourne and Sydney, is becoming more widespread; *Periplaneta brunnea* (Fig. 19.8b) occurs in Qld and N.T., and *Neostylopyga rhombifolia* is found in the N.T. These are all Blattidae-Blattinae. Among the Blattellidae, *Blattella germanica* and *Supella longipalpa* are widespread domiciliary pests, *Shawella coulouniana* (Fig. 19.8i) may be able to adapt indoors, and a few other native species sometimes enter houses. *Shelfordina orchidae* damages orchids in greenhouses. Some Blaberidae also are pests: *Nauphoeta cinerea* (Oxyhaloinae) usually is found in fowl-houses and grain stores. *Pycnoscelus surinamensis* (Pycnoscelinae), a circumtropical species originating in the Indo-Malayan region, is found under stones, manure, wood and rubbish, or burrows in sand or soil; in Australia it also is found in fowl-houses and grain stores. It has been known to damage tobacco plants, tubers of growing potatoes, roots of pineapples, roses and other plants, and often becomes a problem in greenhouses, where it can survive in regions with severe winters. *Diploptera punctata* (Diplopterinae), the Pacific beetle cockroach, is widely distributed in the Indo-Pacific region and has been taken in Australia. In Hawaii it feeds on mangoes, pawpaws and oranges, and also eats the bark from growing branches of certain trees (Roth 1979c).

Some domiciliary cockroaches, especially *B. germanica*, can cause allergic reactions (Roth and Alsop 1978), and have been found to harbour organisms pathogenic to man and other animals (Roth and Willis 1957, 1960). *P. surinamensis* is the intermediate host of the nematode, *Oxyspirura mansoni*, the chicken eyeworm of poultry. Because *P. surinamensis* reproduces parthenogenetically, it can spread easily; the introduction of a single nymph or adult in a suitable habitat can result in its becoming established. In Australia, *N. cinerea* and *P. americana* have been found naturally infected with *Salmonella* (Mackerras and Mackerras 1948), and these cockroaches as well as *P. australasiae*, *P. brunnea* and *S. longipalpa* were experimentally infected with intestinal pathogenic bacteria (Mackerras and Pope 1948).

Special Features of the Australian Fauna

The largest families world-wide are the Blattidae, Blattellidae and Blaberidae, and this also is true of the Australian fauna. Cosmopolitan species aside, many of the Australian taxa are endemic; notable among these are most Blattidae, most epilamprine and panesthiine Blaberidae, and many Blattellidae. Of the Australian Blattidae, *Methana* is found in the Oriental region, *Polyzosteria* occurs in the Oriental region, New Zealand and New Caledonia, *Tryonicus* is in New Caledonia, and *Celatoblatta* (= *Austrostylopyga*) is in New Zealand. All other recorded blattids seem to be confined to Australia where they are particularly abundant in the southern, central and western parts of the continent. The blattellid *Shawella coulouniana* was introduced from Australia into New Zealand where it has become established (Johns 1966). A few blattellids from Qld are also found in New Guinea (Roth unpubl.). The monotypic family Cryptocercidae is confined to North America and eastern Asia.

CLASSIFICATION

Order BLATTODEA

(428 Australian species)

BLATTOIDEA (209)

1. Blattidae (209)
- Cryptocercidae (0)

BLABEROIDEA (219)

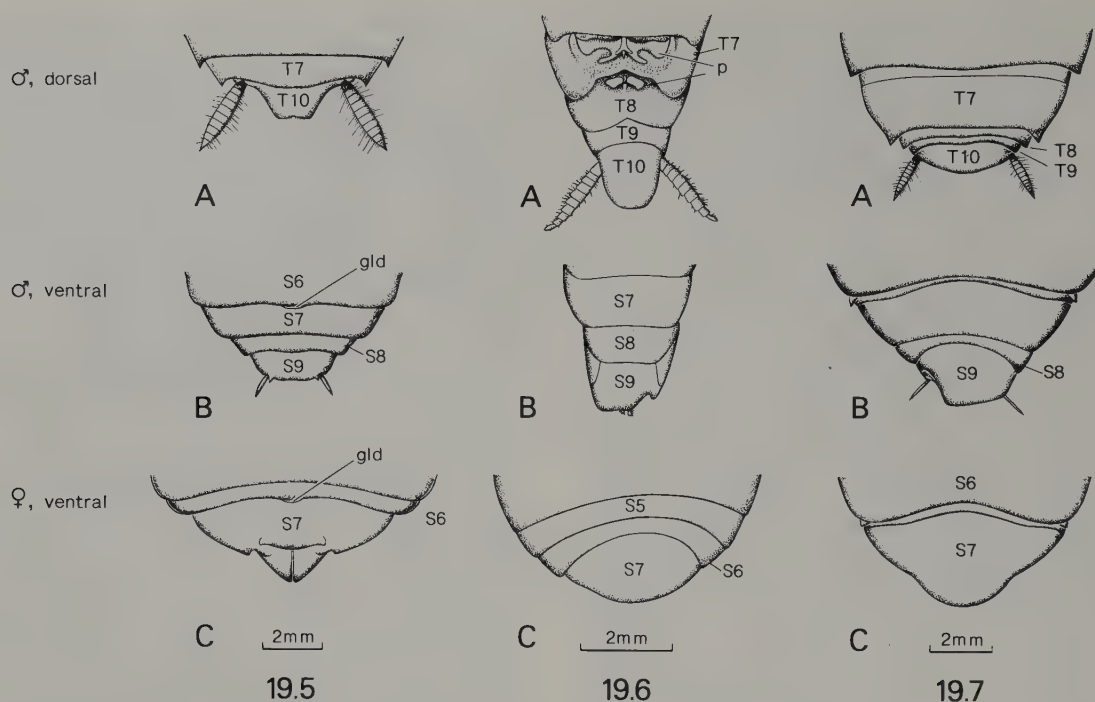
2. Polyphagidae (5)
3. Nocticolidae (2)
4. Blattellidae (140)
5. Blaberidae (70)

There is considerable disagreement in the nomenclatorial treatment of these insects and three modern attempts at cockroach systematics differ markedly in their conclusions regarding the number of higher categories. Princis (1960) using classical morphological characters (wing venation and folding, leg spines, male subgenital plate, etc.), reorganised and extended Handlirsch's system and recognised 4 suborders, 28 families and 21 subfamilies. In sharp contrast, McKittrick (1964) studied several more conservative characters (female genitalia and musculature, male genitalia, proventriculus, oviposition behaviour) and recognised 2 superfamilies, 5 families and 20 subfamilies. McKittrick and Mackerras (1965) added the Tryonicinae. The latest attempt at revising, but not simplifying, the classification is that of Vickery and

Kevan (1983). They dealt chiefly with cockroaches from Canada and adjacent regions, and classified them into 4 superfamilies, 8 families and 14 subfamilies.

McKittrick's classification is strongly supported by studies of several biological systems (Roth 1970), although additional families probably will be necessary. Her system was essentially followed by M. J. Mackerras in the 1st edition and is followed here. Rentz and Cameron (1983) have provided a useful catalogue of the Australian genera and species.

In recent years the taxonomy of various groups of Australian cockroaches has been studied by Hebard (1943), Princis (1954, 1963), M. J. Mackerras (1965a-68d), Roth and Princis (1973) and Roth (1977, 1982a, 1987a,b, 1988, 1990a,b).



Figs 19.5–19.7 Distal segments of abdomen: 19.5 *Platyzosteria nitidella*, Blattellidae; 19.6 *Blattella germanica*, Blattellidae; 19.7 *Laxta granicollis*, Blaberidae. gld, opening of sternal scent gland; p, specialised pits on T7 and T8 [F. Nanninga]

Key to the Families of Blattodea Known in Australia

ADULTS

1. Very small, delicate, white or pale yellow. Males, if fully winged, with both fore and hind wings membranous, hyaline, pubescent, veins unbranched and reduced in number; tegmina may be reduced in length, hind wings vestigial or absent. Female apterous. Male abdomen unspecialised or with a gland on T4. Anteroventral margin of fore femur with a row of piliform setae, terminating in long spine (usually cavernicolous) **Nocticollidae**
Not as above 2
- 2(1). Fully winged males with anal area of hind wing not folded in repose; thickened clypeal shield some-times present **Polyphagidae**
Tegmina and wings reduced (Figs 19.8C, 8F, 11E) or absent (Figs 19.8A, D, 11C), or if fully developed, anal area of hind wing folded fanwise in repose, or with a large apical triangle folded longitudinally and then reflected over the rest of the wing; thickened clypeal shield absent 3
- 3(2). Male styles simple, symmetrical (Figs 19.1, 5B); left lateral phallomere with an extensible hook, right phallomere heavily sclerotised, often with processes, a smooth lobiform ventral phallomere present (Fig. 19.3C). Female subgenital plate bivalvular (Fig. 19.5C) **Blattellidae**
Male styles asymmetrical or symmetrical (Figs 19.6B, 7B), or one or both absent; genital phallomeres much simpler than those of the Polyphagidae or Blattellidae; reversible hooklike phallomere on right or left side; median phallomere (virga) rodlike. Female subgenital plate not bivalvular (Figs 19.6C, 7C) 4
- 4(3). Size usually small to medium; antennae longer than half body length; legs relatively long, slender, spiny; cerci fairly long, tapering, extending well beyond body. Male styles usually present; hooklike genital phallomere on right or left sides. Oviparous **Blattellidae**
Size usually medium to large, females broad bodied (Figs 19.11C, 11E); antennae often less than half body length; legs usually short and stout; femora and tarsi sometimes smooth; cerci often short, some-times unsegmented, not reaching hind margin of supra-anal plate or projecting slightly beyond it. Male styles present or absent; hooklike genital phallomere on right side. Female with an extensible brood sac or atrium (Fig. 19.3A) in which the eggs are incubated. Ovoviviparous or viviparous **Blaberidae**

Superfamily BLATTOIDEA

1. Blattellidae. Anteroventral margin of fore femur usually with many spines, few on posterior margin, mid and hind femora with some spines on both margins; in Tryonicinae, spines on the fore femur reduced in size and number. Wings, when present, with apical triangle; R

with numerous branches, often subdivided; CuA with numerous branches running towards apical margin (Fig. 19.2C). Male subgenital plate often rectangular, styles symmetrical, slender, cylindrical, widely separated (Fig. 19.5B); paraprocts unmodified; sexual tergal gland absent, or present on T1 only where it may be hidden by the hind

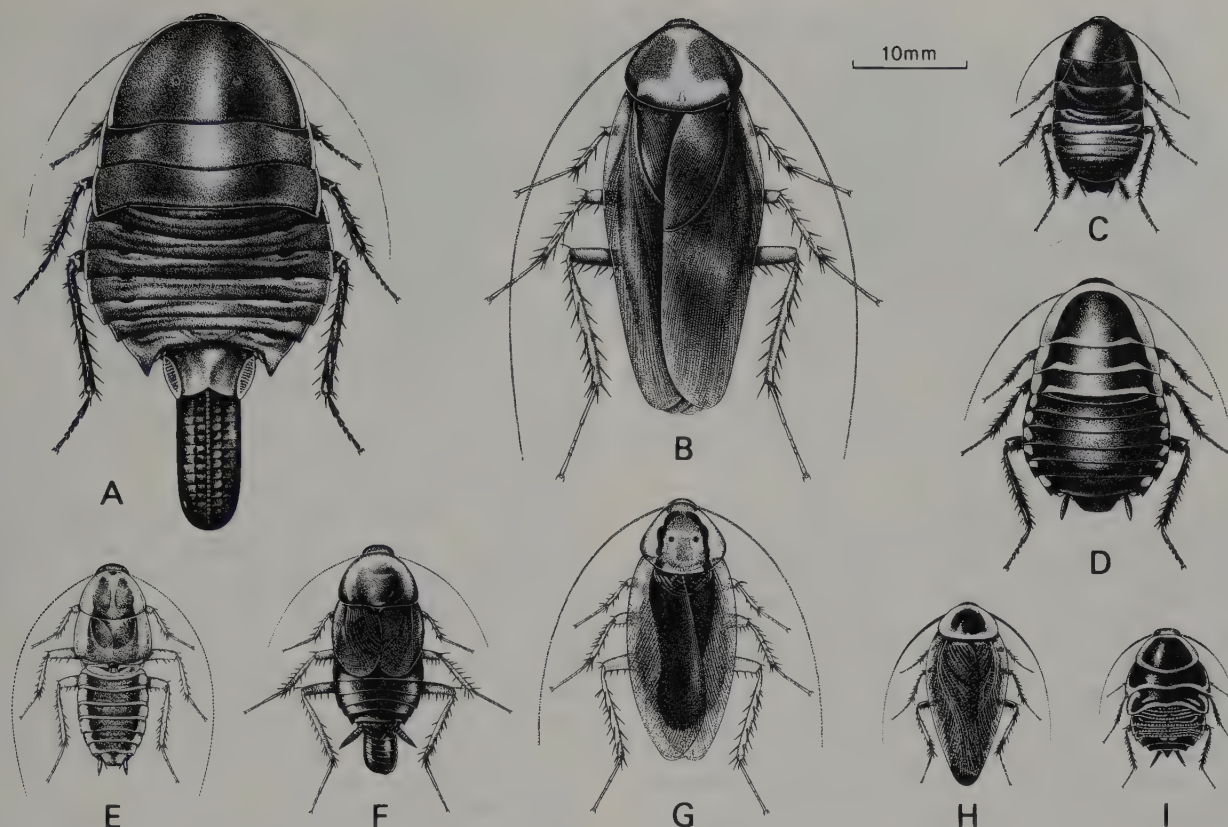


Fig. 19.8 A, *Polyzosteria limbata*, ♀, Blattidae, with ootheca; B, *Periplaneta brunnea*, ♂, Blattidae; C, *Platyzosteria nitidella*, ♂, Blattidae; D, *Cosmozosteria subzonata*, ♀, Blattidae; E, *Temnelytra truncata*, ♂, Blattidae; F, *Shawella coulouniana*, ♀, Blattellidae, with ootheca; G, *Methana curviger*, ♂, Blattidae; H, *Ellipsidion australe*, ♂, Blattellidae; I, *E. australe*, nymph, Blattellidae. [F. Nanninga]

margin of the metanotum. Female subgenital plate (S7) with posterior part modified to form 2 lobes or valves which are united medially by an extensible membrane and partly separated from the rest of the sternum by a transverse suture (Fig. 19.5C). Supra-anal plate of both sexes rectangular, rounded or triangular; cerci often short or flattened, but may taper and project well beyond the supra-anal plate. At ovulation there are 2 yolk-filled oocytes in each ovariole. The ootheca is held vertically with keel dorsad (Fig. 19.8A) and is not rotated prior to deposition. The egg cases of the Polyzosteriinae and Blattinae are very similar, with characteristic, serrated keels (Figs 19.4A, 19.8A) (Roth 1968b).

World-wide there are 4 subfamilies with 44 genera and about 525 species. The Lamproblattinae are principally South American. *Tryonicus* (TRYONICINAE) occur in Australia (3 spp.) and New Caledonia (Roth 1987a). BLATTINAE (5 Australian spp.) include cosmopolitan, domiciliary pests in *Blatta*, *Periplaneta* and *Neostylopyga*. Many POLYZOSTERIINAE (14 genera, 201 spp.) have become adapted to extremely harsh climatic conditions. All except *Methana* (Figs 19.4, 8G) are flightless, but *Scabina* and *Temnelytra* (Fig. 19.8F) have short, quadrate tegmina, and some species of *Platyzosteria* (Fig. 19.8C) have vestigial tegmina. *Polyzosteria* (Fig. 19.8A), *Cosmozosteria* (19.8D), and other genera are apterous (M. J. Mackerras 1965a–c, 1966a,b, 1967a,b, 1968a,b).

Key to the Subfamilies of Blattidae Known in Australia

1. Tarsi usually short, bare, or with hind and sometimes mid metatarsi spined, occasionally 2nd hind tarsal segment spined, 3rd hind tarsal segment bare; pulvilli and arolia usually large, claws usually asymmetrical, sometimes symmetrical or almost so POLYZOSTERIINAE
- Tarsi usually long, all metatarsi spined, sometimes also 2nd and 3rd hind tarsal segments; pulvilli and arolia small, or sometimes arolia absent; claws symmetrical 2
- 2(1). Small; male either with tegmina reduced or absent and hind wings smaller or absent or apterous; femoral spines reduced in size and number, usually only 1 spine on anteroventral margins of mid and hind femora; cerci short, stout, tapering abruptly to fine points which do not project much beyond supra-anal plate in males TRYONICINAE
- Medium sized or large; tegmina and hind wings fully developed or reduced; all femora spined; cerci usually long, tapering gently and projecting well beyond supra-anal plate in both sexes BLATTINAE

Superfamily BLABEROIDEA

2. **Polyphagidae.** Most primitive family of the superfamily. Spines may be absent on the anterior and posterior margins of mid and hind femora. Tegmen sometimes with

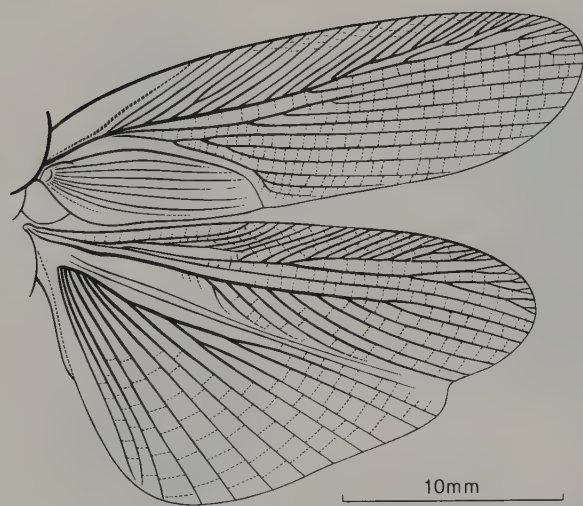


Fig. 19.9 *Neotemnopteryx australis*, Blattellidae, right tegmen and wing.
[F. Nanninga]

reduced venation, or with a network of veins. Anal area of wing reduced and not folded fanwise in repose. Many have a postclypeal swelling and sometimes very large, protruding ocelliform spots. Male tergal glands absent in Australian taxa and rarely occur in others. Female subgenital plate sometimes bivalvular. Each ovariole contains 2 or 3 yolk-filled oocytes at ovulation. The oothecae have keels and a variably developed flange on the anterior end which is held by paraprocts prior to deposition (this based on non-Australian species since no Australian polyphagid oothecae have been described).

World-wide there are about 39 genera and 192 species, many of them desert forms. *Tivia* (2 spp.), *Austropolyphaga* (2 spp.) and *Polyphagoides* (1 sp.) occur in Australia (M. J. Mackerras 1968d).

3. Nocticolidae. The important characteristics are given in the family key. Most are cavernicolous but at least some are termitophilous, and others are epigeal. The eyes may or may not be reduced, but usually are represented by a few ommatidia in cave dwellers. The female's subgenital plate is bivalvular. There are 2 Australian species of *Nocticola*, both from North Qld; one is cavernicolous in the Chillagoe Caves, and the other was taken in a rainforest light trap at Babinda (Roth 1988).

4. Blattellidae. Legs long, slender, spiny, ventral surfaces of tarsi spined. Tegmina and wings fully developed or with reduced wings in both sexes, sometimes with small tegmina only. In fully alate forms, hind wings with or without an apical triangle; R usually well developed, with simple, regularly spaced anterior rami; CuA unbranched (simple), or with complete branches only, or with both complete and incomplete rami. Male abdominal terga unspecialised, or with 1 or 2 modified terga used in sexual behaviour (Fig. 19.6A). In Australian blattellids, the glands when present usually occur on T1, or T1 and T7, or rarely on T7 and T8, or T3, or T4, or T10 (supra-anal plate). Sometimes the morphology of the gland is diagnostic for a genus (e.g. *Escala*). Male subgenital plate (S9) asymmetrical (Fig. 19.6B) or symmetrical, usually

with 2 styles. Female subgenital plate broad, rounded (Fig. 19.6C), rarely bivalvular (e.g. *Anaplecta*, 3 spp. of which are found in Qld and N.T.) Oviparous and ovoviparous.

World-wide this is the largest family with about 209 genera and about 1740 species. In Australia there are about 20 genera of which *Balta* (42 spp.) and *Ellipsidion* (24 spp.) are the largest. [Rentz and Cameron 1983]

5. Blaberidae. Legs often very short; femora and tarsi sometimes without spines. Hind wing with branches of R sometimes reduced to 5 or less; CuA with numerous branches, many going to the plical fold (Fig. 19.10). Visible male tergal glands generally absent. Male subgenital plate asymmetrical or symmetrical, usually bearing a pair of short slender styles (Fig. 19.7B), except in the Panesthiinae which lack them. Hook-like genital phallomere on right side. Female subgenital plate broad, rounded (Fig. 19.7C), notched or truncate, never bivalvular. Cerci usually short. Only 1 yolk-filled oocyte in each ovariole at ovulation. Except in 4 panesthiine genera which do not form an ootheca, all make an egg case and retract it into a uterus. One viviparous genus (*Diploptera*), remainder ovoviviparous.

World-wide this is the second largest family and contains about 155 genera and about 1020 species. The family is poorly represented in Australia, although 6 of the 9 subfamilies occur.

PANESTHIINAE (incl. Geoscaphinae; 22 spp.) are Oriental and Palaearctic, with an extension into Australia where some specialised genera have evolved (Roth 1977, 1979a,b, 1982a). They are stoutly built insects with hard pitted integument, and are adapted for burrowing in wood or soil. The coxae and femora are hairy, and the femora almost devoid of large spines; tibiae strongly spined, sometimes fossorial; tarsi relatively short, without spines, segments 2–4 subequal, terminal segment long with symmetrical claws and no arolia. When wings are present, R has not more than 5 branches. Fully-winged *Panesthia* that are collected in the field usually have only the bases of their flight organs intact. Two or 3 days after eclosion, the more fragile distal parts of the tegmina and wings begin to tear, and fragments are broken off against the wood of the galleries in which these insects live (Redheuil 1973). The wings become fragmented leaving

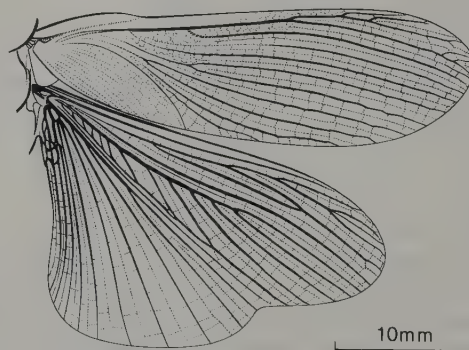


Fig. 19.10 *Panesthia australis*, Blaberidae, right tegmen and wing.

[F. Nanninga]

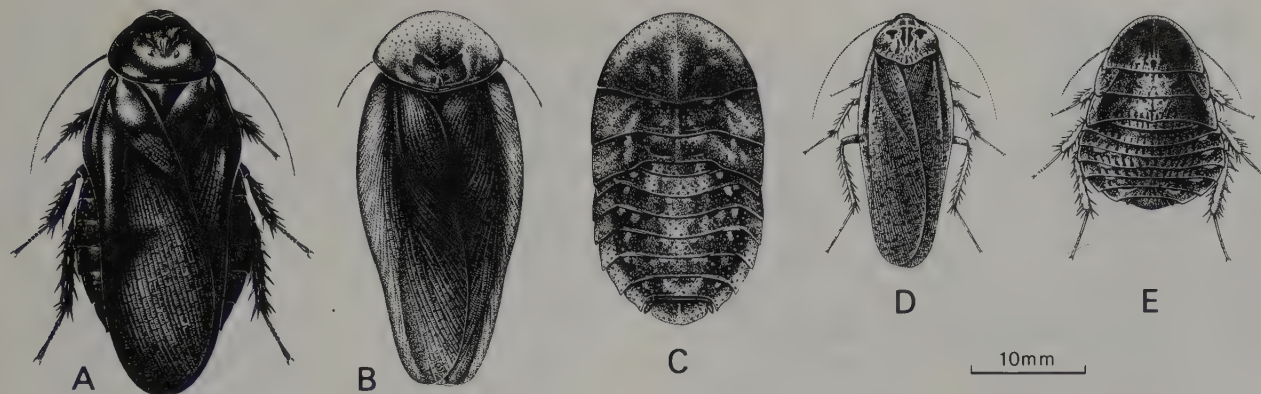


Fig. 19.11 Blaberidae: A, *Panesthia australis*, ♀; B, *Laxta granicollis*, ♂; C, *L. granicollis*, ♀; D, *Calolampra irrorata*, ♂; E, *C. irrorata*, ♀. [F. Nanninga]

only stumps with a very irregular border. Male styles absent. Cerci 1-segmented.

Panesthia (11 Australian spp.) is the most widespread and abundant genus of the subfamily. *P. laevicollis* and *P. australis* (Fig. 19.11A) are common in rotten logs. Unlike the extralimital, wood-feeding *Cryptocercus* which have flagellate intestinal protozoa to digest wood, *Panesthia* utilise intestinal amoebae to digest cellulose. *P. cribrata* is gregarious, whereas *Cryptocercus* live in family groups (Rugg and Rose 1984c). *Macropanesthia* (4 spp.) and *Geoscapheus* (2 spp.) include large apterous forms which burrow in the soil. *G. robustus* occurs in large numbers in burrows, a couple of feet underground, where the adults make a small chamber and live and rear their nymphs. Apparently the adults drag dead leaves and surface litter down to the chambers for food. When disturbed, *Macropanesthia rhinoceros* suddenly expires air producing a hissing noise (Day 1950). This type of sound production is made by Madagascan species of *Gromphadorhina* which hiss by expelling air through the second abdominal spiracle (Roth and Hartman 1967). Other panesthiine genera found in Australia are: *Ancaudellia* (1 sp.), *Neogeoscapheus* (2 spp.), *Parapanesthia* (1 sp.) and *Salganea* (1 sp.). [Roth 1977; Rugg and Rose 1984b]

EPILAMPRINAE (44 spp.). This subfamily is widely distributed in Asia and South America, but only *Calolampra* (28 spp.), *Laxta* (5 spp.), *Neolaxta* (3 spp.), *Ataxigamia* (3 spp.), *Rhabdoblatta* (3 spp.) and *Molytria* (2 spp.) have been reported from Australia.

Calolampra (Roth and Princis 1973) have the dorsal surface smooth and characteristically speckled. They strongly resemble species of *Epilampra* (South America) and *Pseudocalolampra* (Africa). Generally males have fully developed tegmina and wings (Fig. 19.11D), are rarely brachypterous or apterous, and frequently are collected in light traps. Females have lobiform tegmina (Fig. 19.11E) and usually are found in soil. *Molytria inquinata*

is large and speckled. *Ataxigamia tatei* has remarkable long silky hairs on the thorax. *Laxta* contains very flattened, apterous females whose dorsal surface is covered with irregular nodules, and the head is completely concealed by the pronotum (Fig. 19.11C). Males may be fully winged (Fig. 19.11B), brachypterous or apterous. *L. granicollis* (Figs 19.11B, C) is common under bark or leaf litter. *Neolaxta* is very close to *Laxta* and differs principally in the type of front femoral armament (M. J. Mackerras 1968c; Roth 1987b). There are about 100 species of *Rhabdoblatta* world-wide, but only 3 occur in Australia.

OXYHALOINAE (1 sp.). *Nauphoeta cinerea* is the only member of this subfamily found in Australia. It originated in Africa and has become a circumtropical pest. Males have a sound producing apparatus on the pronotum and base of the costal margin of the tegmina. During courtship they rub the pronotum against the tegmina producing a series of chirps. A number of genera of Oxyhaloinae produce stridulating sounds (Hartman and Roth 1967; Roth and Hartman 1967).

PERISPHAERIINAE (1 sp.). An undetermined *Perisphaerus* is found in the Iron Range of northern Cape York Peninsula. This genus is widespread in Asia, Indonesia, New Guinea, Philippines and on other Pacific islands. Nymphs of some species cling to the undersurface of the mother for at least 2 instars. At this time they are blind, have specialized non-chewing mouth-parts, and presumably are completely dependent on the mother (Roth 1981).

DIPLOPTERINAE and PYCNOSCELINAE are each represented by one Australian species.

ACKNOWLEDGMENTS. I thank the Bureau of Flora and Fauna, Australian Biological Resources Study, for partial support, and the late M. J. Mackerras for material taken from her chapter on cockroaches in the 1st edition of this book.

Isoptera

(Termites)

J. A. L. WATSON and F. J. GAY

Polymorphic, mandibulate, exopterygote Neoptera, living in social family units composed of a limited number of reproductive forms associated with their offspring, numerous wingless sterile soldiers and workers. Antennae moniliform; wings elongate, membranous, held flat over the body at rest, and capable of being shed by means of basal sutures; cerci short; external genitalia rudimentary or wanting.

This is a relatively small order, closely related to the Blattodea, and occurring mainly in tropical and subtropical regions. It contains over 2300 species, of which 258 described and at least 90 undescribed species occur in Australia. They are soft-bodied insects with cryptic habits, living in family groups (colonies). Each colony contains several castes, morphologically and behaviourally specialised to perform different tasks. Three principal castes are recognised (Fig. 20.1). (1) Reproductives. Primary kings and queens are fully sclerotised individuals derived from winged adults (alates), their wing remnants in the form of four small, triangular scales. Supplementary (or replacement) reproductives (*neotenics*) are usually less heavily sclerotised and either lack wing elements, or have rounded wing buds. (2) Soldiers. Sterile males or females and usually apterous, soldiers have heavily sclerotised heads armed with either large mandibles or a long snout (rostrum or *nasus*) from which threads of sticky secretion are fired. (3) Workers. Generally unpigmented and only lightly sclerotised, these apterous, sterile males or females lack special external modifications.

Immature stages of all these castes may also be present: wing-budded nymphs (reproductive nymphs), potentially fertile; presoldiers (white soldiers); and apterous larvae with small thoraces. Inter castes are also found occasionally (Fig. 20.11).

The alates vary in length from 6–7 mm (small *Amitermes* and *Microcerotermes*) to 17–18 mm (*Mastotermes*) and in wing-span from 12 mm (small *Amitermes*) to 50 mm (*Mastotermes*). The soldiers and workers vary in body length from 2.5 mm (small *Tumulitermes*) to 15 mm (*Porotermes* and *Neotermes*).

World literature on termites has been abstracted by Snyder (1956–68), Ernst and Araujo (1986) and, from 1979, in *Termite Abstracts*. Snyder (1949) catalogued the world fauna. Major synoptic works include Krishna and Weesner (1969, 1970), Harris (1971) and Grassé (1982–86). Lee and Wood (1971) dealt with termites and soils. Several texts include useful documentation of particular aspects of termite biology: Keast *et al.* (1959) (Australian zoogeography and ecology); Brian (1978) (food and feeding, nutrient dynamics, role in ecosystems); Hermann (1979, 1981, 1982) (inquilines, defensive mechanisms); Watson *et al.* (1985) (caste differentiation); and Vinson (1986) (economics and control).

G. F. Hill (1942) monographed the Australian termites. Ratcliffe *et al.* (1952) gave a general account of them, as did Hadlington (1987). Perry *et al.* (1985b) provided a guide to south-western Australian termites, and Watson (1988) to termites in the Canberra region and south-eastern N.S.W.

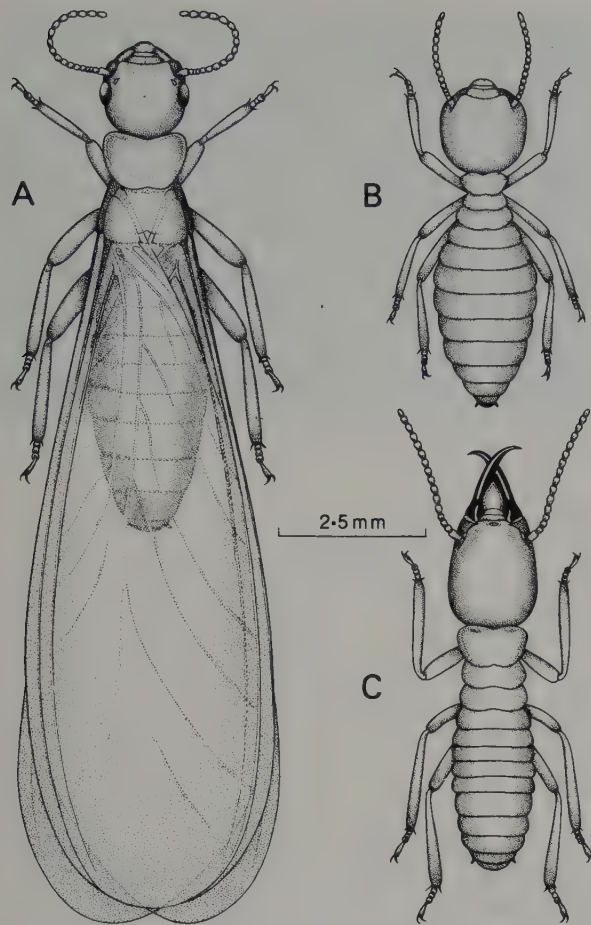


Fig. 20.1 Castes of *Coptotermes acinaciformis*, Rhinotermitidae: A, winged reproductive or alate; B, worker; C, soldier. [B. Rankin]

Anatomy of Adult

Reproductives

Head. Ovoid or rounded, somewhat flattened, often with distinct ecdysial lines. Compound eyes present (reduced, sometimes greatly so, in neotenics). Ocelli present or absent; when present, only 2 (median ocellus absent). Antennae moniliform, of 10–32 segments; number of segments variable within a species and even from side to side of an individual. Labrum well developed. Clypeus divided into distinct ante- and postclypeus. Mouth-parts of typical mandibulate, blattoid type. Mandibles of alates and workers of the same genus closely similar, affording valuable taxonomic characters at familial and generic level, although dietary specialisation may bring about convergence (Ahmad 1950; L. R. Miller 1984a). Large basal plate of labium (*gula* or *gulantum*) also providing useful taxonomic characters. Fontanelle (p. 332) present in Termitidae and Rhinotermitidae.

Thorax. Prothorax with well-defined pronotum. Meso- and metanotum subequal, without distinctive features. Sterna membranous.

Legs. All legs very similar, with large broad coxae, and long slender tibiae armed with terminal spines. Tarsi generally 4-segmented, 5-segmented in *Mastotermes*. Arolium present in some primitive termites.

Wings. Two pairs of elongate, membranous wings; fore and hind similar in shape, except in *Mastotermes* in which hind wing has a pronounced anal lobe of blattoid type (Fig. 20.2). Anterior veins strongly sclerotised, others poorly developed. No cross-veins, but wing membrane sometimes reticulate. Venation reduced and simple (Fig. 20.3), except in *Mastotermes* which has a primitive venational pattern with all veins present (Fig. 20.2). Wings have a basal (humeral) suture, which permits wing

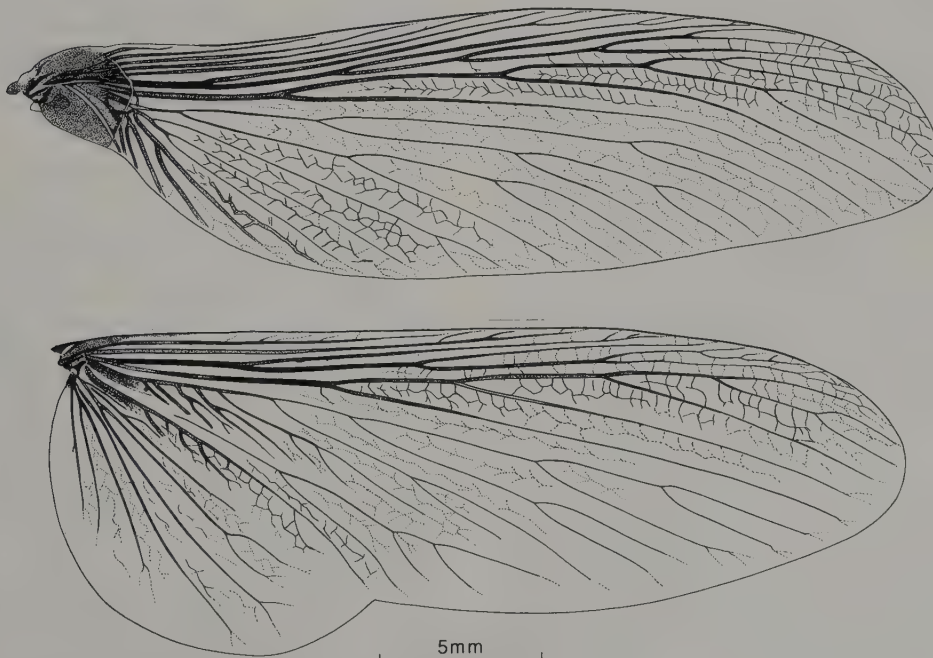


Fig. 20.2 Fore and hind wings of *Mastotermes darwiniensis*, Mastotermitidae.

[N. Key]

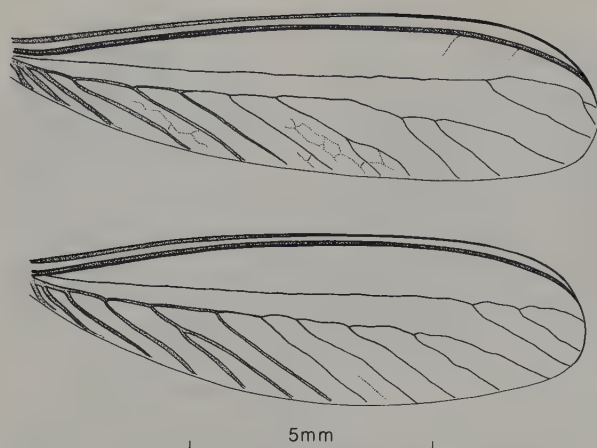


Fig. 20.3 Fore and hind wings of *Nasutitermes dixonii*, Termitidae.

[N. Key]

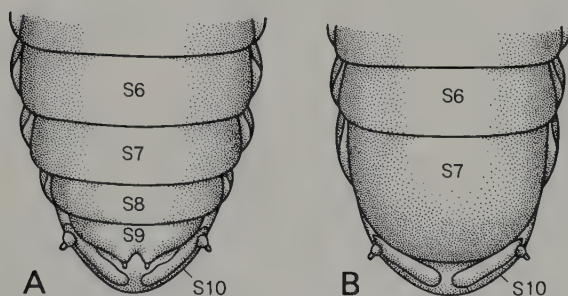


Fig. 20.4 Distal abdominal sterna of alates of *Coptotermes lacteus*, Rhinotermitidae: A, ♂; B, ♀.

[B. Rankin]

shedding and leaves a triangular stump (scale), attached to thorax. This suture is lacking in the hind wing of *Mastotermes*, but there is a compensating line of weakness.

Abdomen. Of 10 evident segments, each with tergum and sternum, except that S1 is absent. All other sterna visible and entire in males, except S9 which is divided longitudinally in some higher termites. S7 enlarged in females to form subgenital plate which obscures remaining sterna, except in Hodotermitidae (Fig. 20.4). Terminal segment with pair of short, 1–5-segmented cerci, present in all castes. A pair of small, unsegmented styles present on posterior border of S9 in males of most species. External genitalia absent except in *Mastotermes*, in which the female has a reduced ovipositor of blattoid type and the male a median, membranous, copulatory organ.

In most termites, the primary and, often to a lesser extent the neotenic, female reproductives exhibit *physogastry*. This is a pronounced swelling of the abdomen resulting from the proliferation of the ovarioles and fat body. The enlargement is accommodated by the unfolding of the highly convoluted intersegmental membranes, so that the contiguous terga and sterna of the alate abdomen come to appear as islands of sclerotised cuticle (Fig. 20.5).

The major function of both primary and neotenic reproductives is to maintain the strength of the colony by providing a regular supply of spermatozoa and eggs.



Fig. 20.5 Physogastric queen of *Nasutitermes exitiosus*, Termitidae; length ca 30 mm.

[J. P. Green]

Soldier

Structurally very specialised. Head greatly developed, often oblong or pyriform, at times exceeding in size the rest of the body. Obsolescent or weakly developed compound eyes present in some primitive genera, absent elsewhere. Antennae moniliform, sometimes tending to filiform, of 10–26 segments. Soldiers genetically male or female, sometimes predominantly or entirely one or other, but secondary sexual characters recognisable only in some primitive genera. Gonads almost always vestigial.

Two distinct types of soldiers are recognisable: (1) mandibulate, with well-developed jaws often grotesque in form; (2) nasute, with the head produced anteriorly into a rostrum, and with small or vestigial jaws (Fig. 20.6). In most species, soldiers are of one size. In some kalotermitids and termopsids, their size is diverse, even within a colony, and in rhinotermitids and termitids there may be well-defined di- or trimorphism in size and shape, as in *Schedorhinotermes* and many species of *Nasutitermitinae*. This variability depends on the age and, often, the sex of the precursor stage (Watson *et al.* 1985) (p. 335).

A well-developed frontal gland is present in the

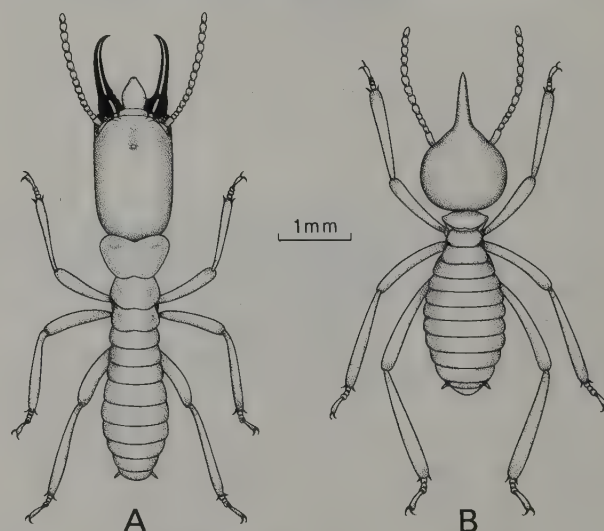


Fig. 20.6 A, mandibulate soldier of *Heterotermes ferox*, Rhinotermitidae; B, nasute soldier of *Nasutitermes exitiosus*, Termitidae.

[B. Rankin]

Rhinotermitidae and Termitidae; it occupies a variable portion of the head, and in *Coptotermes* also extends well into the abdomen. The secretion from this gland is exuded through a pore on the frontal region of the head (*fontanelle*). In nasute soldiers the duct from the frontal gland opens at the tip of the rostrum, and the secretion is emitted either as a droplet or as a fine thread. In soldiers of *Parrhinotermes* and *Schedorhinotermes* the secretion flows from the fontanelle down the frontal gutter to a fringe of hairs on the anterior border of the labrum; from there it is smeared on to the intruder (Deligne *et al.* 1981).

The primary function of the soldier caste is to protect the colony. This may be achieved mechanically by biting, as in mandibulate soldiers; by blocking access galleries with their heavily sclerotised heads, which are specifically adapted for this purpose (*phragmotic*) in one or two genera; or by chemical means in those forms that have functional frontal glands. The frontal gland secretion may be toxic or repellent to invading insects, such as ants, or may be tacky and entangle their legs and antennae. The protective activities of soldiers are most noticeable during building or repair operations on the nest, or during the release of winged reproductives from it. At such times conspicuous numbers are present at all breaches of the nest or gallery system.

Worker

Structurally unspecialised. Body usually pale and only lightly sclerotised. Mandibles strongly sclerotised, differing little from those of reproductives (Fig. 20.14). Eyes usually absent. Pronotum similar in form to that of soldier. Both sexes represented in most species, but gonads vestigial. Worker polymorphism common, based on age and sex.

Workers are numerically the largest caste in the colony. Their functions include gathering food; feeding the young, the soldiers, the reproductive nymphs and the reproductives; tending the eggs; and repairing and enlarging the nest and gallery system. Older workers may predominate in activities outside the nest.

Internal Anatomy

The only organ system that exhibits obvious special features, certain of which are associated with the termite's way of life, is the alimentary canal. This is a convoluted tube of moderate length, similar to that of the Blattodea (Fig. 20.7). The fore gut consists of an oesophagus and a more or less distended crop which terminates in a muscular proventriculus with sclerotised spiny folds. The mid gut is relatively short, with or without anterior caeca. The Malpighian tubules (4 in Termitidae, usually 8 or 9 in other families except Mastotermitidae which has up to 15) are attached at the junction of mid and hind gut. The first section of the hind gut terminates in a muscular, often spiny, enteric valve. The next section forms a distended paunch, its posterior part tapering to a more or less distended colonic region. The rectum has a six-fold symmetry and is preceded by a constricted, often spiny, rectal valve.

Except for the number of caeca and Malpighian

tubules, the alimentary canal is generally similar in form in all families except the Termitidae. In termitids, particularly in genera that feed on material other than relatively sound wood, the gut shows various modifications. In all subfamilies an extension of part of the mid gut overlaps the foremost section of the hind gut, forming the so-called mixed segment. All sections of the hind gut are elongated to some degree, particularly in soil-feeding termites, and may be variously dilated. The paunch may be subdivided into two distinct sections. These variations in gut structure provide useful taxonomic characters (cf. L. R. Miller 1984a,b, 1991).

Immature Stages

Egg. Pale yellow or white in colour, reniform and about 0.75 to 1.25 mm in length. Eggs are normally laid singly, and may be collected by the workers into irregular masses in the nest; but in *Mastotermes* they are laid in batches of up to 24 arranged in two regular rows in a structure somewhat resembling the ootheca of cockroaches (Fig. 20.8).

Caste Development. Developmental pathways are complex and variable in termites (Watson *et al.* 1985). There is a primary separation into reproductive and non-reproductive lines, commonly expressed at the moult of the first larval stage (Fig. 20.9), but not externally marked until the second moult in rhinotermitids, and rarely shown in kalotermitids or termopsids. The reproductive line shows typical exopterygote development leading to the alate and, as a rule, to the neotenic. The non-reproductive line includes one or more further larval stages leading to the workers and, via an intermediate presoldier stage (Fig. 20.10c), to the soldier. In *Mastotermes*, neotenics develop from workers, in one moult. The kalotermitids and, apparently, termopsids have a remarkably flexible system involving moults in which differentiation is reversed, stationary moults where there is no change, and moults in which intermediate stages are inserted or omitted from the normal pathway. Reversionary moulting appears to be peculiar to these two families, but stationary and irregular moulting occur in other termites. Caste development is more rigid and stereotyped in rhinotermitids and, particularly, termitids, and sexual dimorphism is common.

Biology

The Colony. Colony founding is normally initiated by the release of large numbers of alates from the parent colonies at a particular time of the year, and even at a particular time of the day. In Australia there are two main flight periods, late spring to early summer, and autumn. The release of winged reproductives of both sexes may be spread over a period of several weeks during which small batches of alates emerge at irregular intervals, or it may be concentrated into a brief period of a few days with most of the alates departing in a single colonising flight. It is not uncommon for all nests of a particular species in one district to release their alates simultaneously. The alates contain large quantities of stored nutrients, particularly lipids, and their water content is low. They are weak

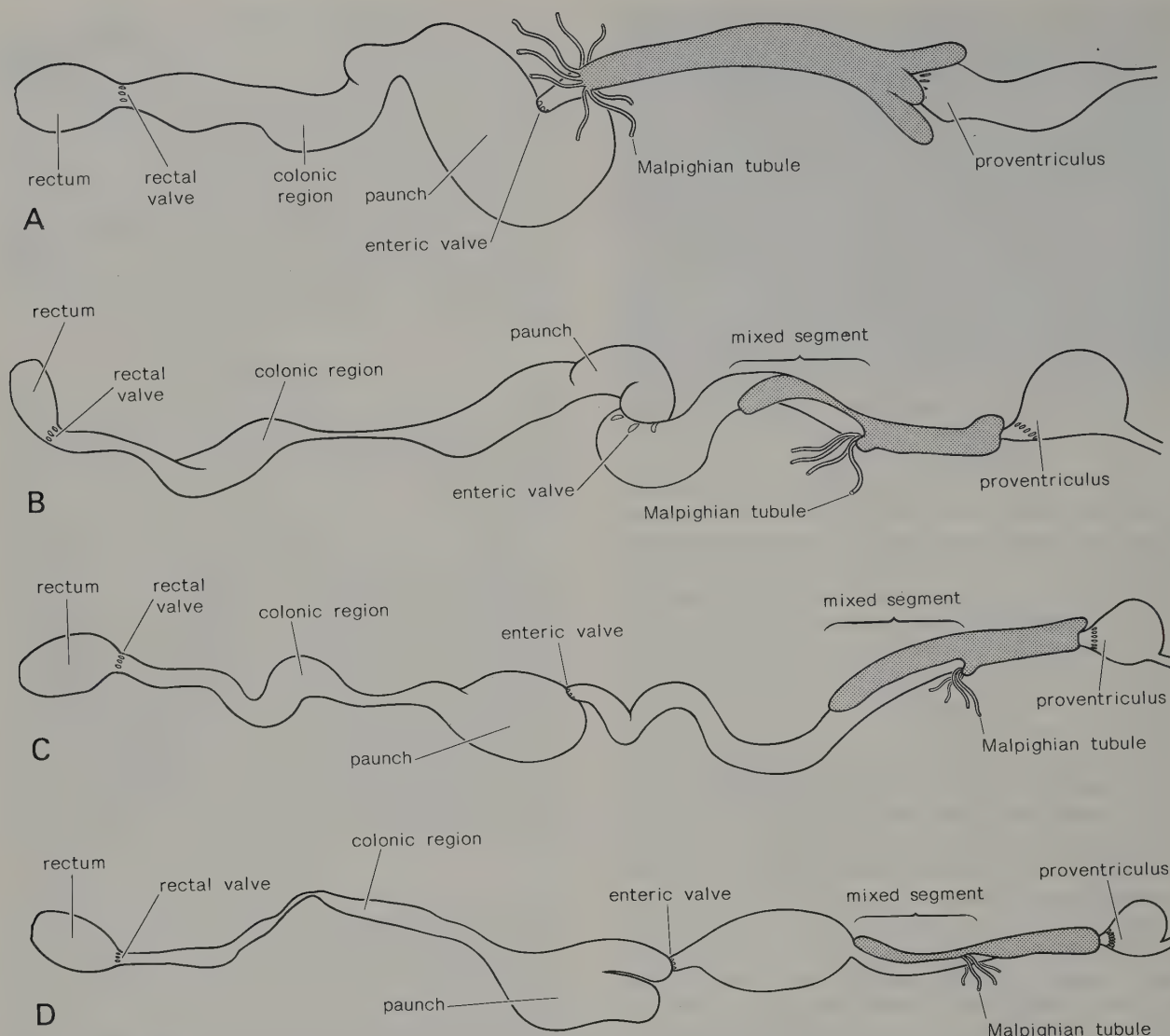


Fig. 20.7 Gut structure in worker termites: A, *Porotermes adamsoni*, Termopsidae; B, *Macrognathotermes sunteri*, Termitidae; C, *Apsenterotermes iridipennis*, Termitidae; D, *Amitermes* sp., Termitidae. Not to scale. [S. Smith]

fliers, and the colonising flight is generally of short duration and distance, unless assisted by wind. The wings are shed at the basal suture soon after alighting, and the de-alated females attract males by elevating the abdomen and presumably emitting a sex-attractant pheromone. Pairs of males and females then form tandems which seek out suitable sites for new colonies in soil or wood. The royal pair excavate then seal themselves into a small nuptial chamber. They then copulate, often repeatedly. They commonly become aggressive towards others of their species and, although they do little to feed themselves, they may drink large amounts of water, which they store (Watson *et al.* 1972).

The primary queen may begin to lay eggs within a few days of mating, but the initial batch is small and rarely numbers more than about 20. These hatch after some weeks, and this primary brood is tended by the king and queen during its early development. Oviposition is commonly resumed as the progeny develop the ability to

maintain themselves, and to feed the queen. Ultimately egg production becomes an almost continuous process, at least during the warmer times of year, and mature physogastric queens of such species as *Nasutitermes exitiosus* and *Coptotermes lacteus* are capable of laying 2000–3000 eggs per day.

Species which readily form neotronics may found new colonies by fission, following which the isolated groups can develop their own reproductives.

Only workers and soldiers are produced in young



Fig. 20.8 Egg mass of *Mastotermes darwiniensis*, Mastotermitidae.

[B. Rankin]

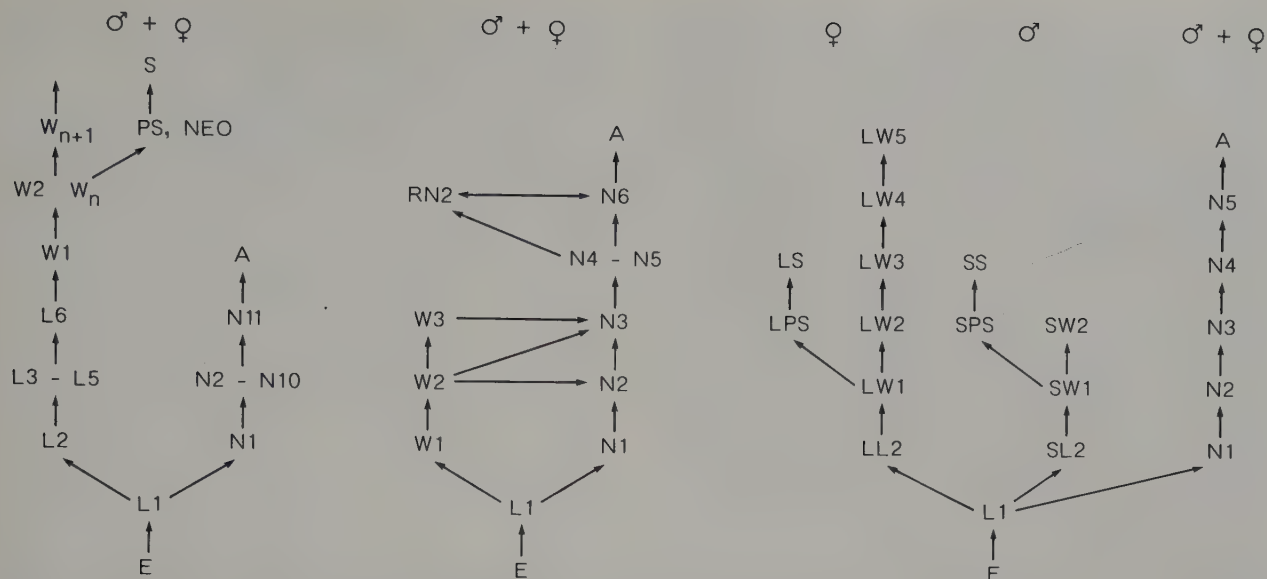


Fig. 20.9 Developmental pathways of termites: left, *Mastotermes darwiniensis*, Mastotermitidae; centre, *Kalotermes rufinotum*, Kalotermitidae; right, *Nasutitermes exitiosus*, Termitidae. A = alate; E = egg; L = larva; N = nymph; NEO = neotenic; PS = presoldier; RN = reverted nymph; S = soldier; W = worker. Prefixes L and S indicate large and small L, PS, S and W; numbers indicate stages. [S. Smith]

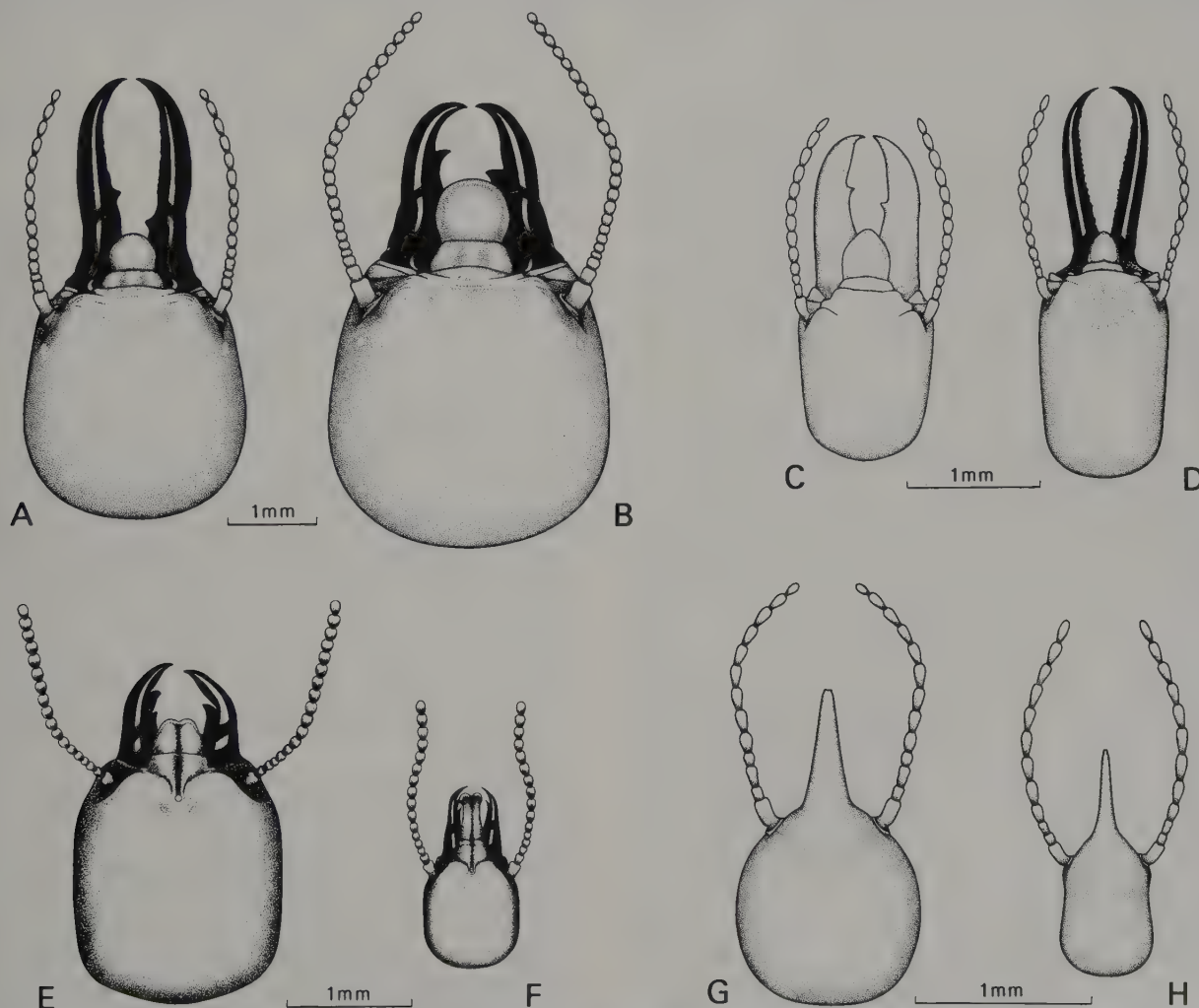


Fig. 20.10 Heads of: A, B, soldiers of *Mastotermes darwiniensis*, Mastotermitidae, nanitic (A) and mature (B); C, presoldier and D, soldier of *Microcerotermes boreus*, Termitidae; E, large (major) soldier of *Schedorhinotermes actuosus*, Rhinotermitidae; F, small (minor) soldier of *S. intermedius*; G, H, large and small soldiers of *Tumulitermes recalvus*, Termitidae. [B. Rankin]

colonies. The early broods are also distinctly undersized (*nanitic*) and the soldiers may differ in form (Figs 20.10A, B). Alates do not appear until the colony is several years old. Mature colonies, which take many years, or even decades, to develop, may range in size from a few hundred individuals, as in many kalotermitids, to a million or more, as in *Mastotermes*, some species of *Coptotermes*, and some Termitidae.

Both of the primary reproductives may live for many years [at least 17 in *Mastotermes* (Watson and Abbey 1989)] and during this time the queen is periodically fertilised by the king. Normally there is only a single primary king and queen per colony, the founding pair, but instances of multiple primary queens are known in species of *Nasutitermes*. These are probably replacement reproductives for, at least in *N. exitiosus*, lost primaries are replaced by alates retained in the nest and dewinged (Watson and Abbey 1985).

Little is known of the age of termite colonies in Australia. A *Nasutitermes triodiae* mound near Pine Creek was probably inhabited for a century or more, and *Drepanotermes perniger* colonies can apparently survive for more than 50 years (Watson *et al.* 1988). Indeed, the colony is potentially immortal in species that have the ability to replace lost reproductives.

Neotenicis are, as a rule, absent in colonies in which the primary reproductives are still present. Mature colonies of *Mastotermes* are headed by numerous neotenicis, and the replacement queens produce more but smaller eggs than primaries. In other termites, neotenicis are often less fecund than the primary queens, and multiple replacements may be needed to maintain the strength of the colony (Lenz *et al.* 1988a). More than 100 neotenic queens have been recorded from a colony of *Amitermes laurensis* and over 50 from a colony of *Protocapritermes krisiformis*.

In mature colonies, the proportion of soldiers to workers, or to nymphal forms performing worker functions, varies considerably. *Invasitermes* lacks soldiers. In many Kalotermitidae and in some species of *Amitermes* the proportion is less than 1 per cent, whereas in some species of *Nasutitermes* it may be as high as 15 per cent. These sterile castes are comparatively long lived; soldiers and workers of *N. exitiosus* are known to live at least two years, and those of *Coptotermes acinaciformis* for up to four years.

Termites feed on sound and decayed wood, dry grass, fungi and other materials of vegetable origin, such as dead leaves, bark, humus and soil rich in humic materials, and the dung of herbivores. The principal material utilised is cellulose, although some termites can degrade lignin (Cookson 1988). The mid gut of termites secretes cellulases, which appear to be of primary importance in the utilisation of cellulose (Hogan *et al.* 1988). In all families but the Termitidae these are supplemented by enzymes (including cellulases) secreted by symbiotic flagellate Protozoa in the hind gut, producing acetate and butyrate as end products; in termitids, anaerobic bacteria there may do much the same, although they are not cellulolytic (O'Brien and Slaytor 1982). Termites can fix atmospheric

nitrogen, apparently a function of the hind gut bacteria, but the capacity is labile (Lovelock *et al.* 1985), and its significance for the termite is obscure.

Most termites consume their food *in situ*, but many species that feed on grass or plant litter harvest their food and carry it back to the nest. This occurs throughout the genera *Drepanotermes* and *Tumulitermes* so far as is known, and in some species of *Schedorhinotermes*, *Amitermes* and *Nasutitermes*. In *Amitermes*, harvesting is done under the protective cover of thin mud sheeting built over the grass or litter. The other harvesters come out and forage on the surface on humid overcast days or at night, and the workers and soldiers of the diurnal harvesters are generally heavily pigmented. Some of the harvesting species build mound nests which serve largely as food stores, but others (e.g. many species of *Amitermes*, *Drepanotermes* and *Tumulitermes*) build subterranean nests.

The location of new food sources appears to depend largely on random foraging. However, termites may be able to recognise changes in soil temperature and moisture brought about by fallen logs, and their tunnels often follow drain pipes, facilitating their entry into buildings. Workers and soldiers (and at least in some Central American *Nasutitermes*, soldiers alone) carry out this exploratory activity and eventually return to the central nest with the aid of scent trails, which consist of minute amounts of pheromones produced by sternal glands and deposited on the substrate.

Both stomodaeal and proctodaeal feeding are common in termites. This exchange of food (*trophallaxis*) represents the normal manner in which soldiers, larvae, reproductive nymphs and the reproductives themselves obtain their food and, to some extent, pheromones. In species with symbiotic Protozoa, proctodaeal feeding is essential for the refaunation of individuals that have lost their intestinal fauna during ecdysis.

Sex Determination. Both sexes are diploid, and the chromosomes are small; known numbers range from 14 to 49 pairs (*Mastotermes*; Bedo 1987). An XX-XY system of sex determination is believed to operate, although visible differentiation of sex chromosomes has been recorded in only one species (Luykx 1987). Some kalotermitids and rhinotermitids, including *Neotermes insularis* and *Bifiditermes improbus*, have sex-linked translocations which result in the formation of rings or chains of chromosomes in the male. In extreme cases these may incorporate up to half the autosomes, which then act as sex chromosomes.

Caste Determination. Although relatively little work has been done on caste determination in Australian termites, there is every reason to suppose that principles discovered elsewhere are applicable generally. The most important is that caste is determined by extrinsic factors acting on the individual. It is useful to look first at the differentiation of the reproductive and sterile lines revealed at the end of the first instar, then at the later development of neotenicis and soldiers.

Differentiation at the first larval moult is poorly understood. However, determination probably occurs much

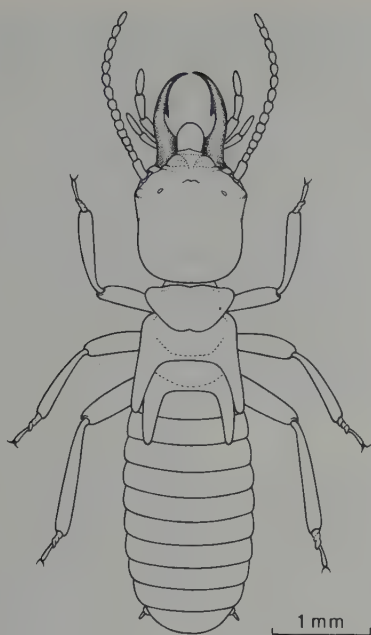


Fig. 20.11 Intercaste between soldier and reproductive nymph] in *Amitermes xylophagus*, Termitidae. [B. Rankin]

earlier: in *Nasutitermes exitiosus*, it is established before laying. The mechanism is unknown, but it is noteworthy that at the time the queen is laying nymph-producing eggs, she is also laying eggs that will develop into workers (Watson and Abbey 1988).

More is known of determination into neotenics and soldiers (Watson *et al.* 1985). Both involve a pheromonal switch of the individual's endocrine system. In almost all the termites studied, these castes apparently secrete pheromones that inhibit the development of further members of that caste. If reproductives or soldiers are lost, the level of the relevant pheromone falls and differentiation into replacements follows. The development of a neotenic can be seen as premature metamorphosis (Fig. 20.9), with the endocrine changes that metamorphosis involves. The development of presoldiers depends on elevated levels of juvenile hormone, an effect known in *Mastotermes* and Australian species of *Coptotermes* and *Nasutitermes*. *Mastotermes* is unique in that existing neotenics stimulate mature workers to become neotenics, the normal end-point of worker development in *Mastotermes*.

In all cases, surplus individuals of a caste are destroyed by the workers.

The existence of intercastes emphasises that individuals retain the potential to form other castes. In Australian termites, intercastes are now known between soldiers and reproductive adults, nymphs (Fig. 20.11) or workers; between presoldiers and neotenics; and between workers and reproductive nymphs.

Polyethism. It is now well established that the chores of worker termites change as they age (McMahan 1979). Thus 4th- and 5th-stage workers of *Drepanotermes*, which are darkly pigmented, forage in the open, often by day, and repair and extend the nest, while the sparsely

pigmented earlier stages remain under cover. Similar polyethism occurs in species of *Nasutitermes*. In the African and Asian genus *Macrotermes*, workers are of one instar, and show age-dependent changes in behaviour comparable to those of honey bee workers.

Large (presumed female) and small (presumed male) soldiers of *Nasutitermes exitiosus* (cf. Fig. 20.9) also differ in behaviour (McMahan 1979). The small soldiers are aggressive whereas the far less numerous large soldiers retreat from disturbance.

Evolution of Sociality in Termites. All termites are fully social (eusocial), but the origin and evolution of their sociality are poorly understood. Termites are closely akin to cockroaches, as the cockroach-like features of *Mastotermes*, and its sharing of otherwise unique symbiotic gut flagellates with the subsocial, wood-eating cockroach *Cryptocercus* suggest. Cockroaches, however, show no diversification of development that could underlie the two developmental lines common to termites; closer parallels can be found in the polymorphism of locusts, aphids and ptiliid beetles (Watson and Sewell 1981). These, however, do not involve sterile castes. No satisfactory genetic models have been developed to account for the selective advantages of sterility in termites, and the eusociality that depends on it.

Nests. Termites build various types of nest. The simplest is that found in the Kalotermitidae and Termopsidae, in which the whole colony lives in a series of galleries and chambers excavated in moist or dry wood and is surrounded by its food (Figs 20.12A, B). Many subterranean forms inhabit similarly diffuse systems of galleries in the soil, apparently without a central nest, as in, e.g., some species of *Amitermes*, *Drepanotermes* and *Tumulitermes*. Others construct a more or less complex central nest in the soil, in a log or stump, or in the trunk of a living tree (Fig. 20.12c). Many economically important termites build nests of this type, notably *Mastotermes* and species of *Coptotermes* and *Schedorhinotermes*.

About one-fifth of the described Australian species of termite build termitaria in the form of mounds, often of very distinctive form. Their size and shape vary: hardened pavements (Fig. 20.12i); low, domed to upright mounds built by many species (Figs 20.12E, G, 13); tall, columnar structures of *Nasutitermes triodiae* which may be more than 7m high (Fig. 20.12H); and the curious wedge-shaped mounds of *Amitermes meridionalis* in which the long axis is always oriented on a north-south line (Fig. 20.12H). In general, each species builds its own characteristic mound but some, such as *N. triodiae* and species of *Drepanotermes*, build distinctly different termitaria in different parts of their ranges. Although termitaria are normally built on or in the ground, one species of *Amitermes* and species of *Microcerotermes* and genera in the *Termes* complex commonly construct their clay-covered nests on poles, posts or the trunks of trees. Tree-nests consisting of dark, carton-like material are built by two species of *Nasutitermes* (Fig. 20.12F).

Although one colony normally occupies a single nest, multiple nests occur, or are the rule, in some termites, including *Mastotermes* and at least some species of



Fig. 20.12 Nests of termites: A, *Porotermes adamsoni*, Termopsidae, in tree trunk ca 0.6 m diameter; B, *Cryptotermes brevis*, Kalotermitidae, in moulding 70 mm wide; C, *Coptotermes frenchi*, Rhinotermitidae, in tree trunk ca 0.6 m diameter; D, *Drepanotermes penniger*, Termitidae, diameter ca 1.0 m; E, *Amitermes vitosus*, Termitidae, to ca 1.5 m high; F, *Nasutitermes walkeri*, Termitidae, ca 1.0 m long; G, *Coptotermes lacteus*, Rhinotermitidae, ca 1.5 m high; H, *Amitermes meridionalis*, Termitidae, ca 3 m high; I, *Nasutitermes triodiae*, Termitidae, ca 5 m high.

[A–C, G, H by J. P. Green; D, E, I by J. A. L. Watson; F by Forestry Commission of N.S.W.]

Coptotermes, *Amitermes*, *Drepanotermes* and *Tumulitermes* (Watson *et al.* 1988). These *polycalic* systems may include a primary nest in which the reproductives live and secondary nests, sometimes acting as food stores. In *Mastotermes*, however, the numerous reproductives can move throughout the nest system.

The internal architecture of the mound varies greatly from species to species. In many species of *Amitermes*, the chambers are fairly much alike, although outer chambers may be used as food stores, as in *Drepanotermes* and

other harvesters. The most complex mounds belong to species of *Coptotermes* and *Nasutitermes* (Fig. 20.13). In these the outer wall is built of soil and, in the case of *Coptotermes*, is massive and hard, with few galleries or chambers. The inner region is generally composed of woody faecal material (*carton*) with a variable admixture of soil, and may contain a nursery in the fragile-walled, densely packed galleries in which the eggs, young and moulting individuals shelter. From it opens a large, flat cell (royal cell) in which the reproductives live.



Fig. 20.13 Mound of *Nasutitermes exitiosus*, Termitidae, ca 1.0 m diameter: A, external appearance; B, sectioned to show internal structure. [J. P. Green]

This complexity of structure enables the termites to maintain a far more constant environment than is possible in simpler nests. Relative humidity is close to saturation in the nursery, and temperatures there are buffered against fluctuation and kept above ambient except during the hottest times of year, when they can be kept below it (Watson and Abbey 1986). The termites' metabolism and behaviour contribute to both. Some degree of temperature regulation is achieved in some simple mounds by orientation, as in meridional mounds of *Amitermes laurensis* (and, presumably, *A. meridionalis*), the shape and alignment of which minimise insolation at the hottest times of day.

From the termitaria subterranean galleries and covered runways extend to distant food sources, commonly 50–75 m in *Coptotermes* and *Nasutitermes*, and 100 m, perhaps to 250 m, in *Mastotermes* (Gay and Calaby in Krishna and Weesner 1970).

The fabric of the termitarium offers a suitable nesting place for other termites, and some have become highly specialised, e.g. *Ahamitermes*, *Incolitermes* and *Invasitermes*. It is not uncommon to find several species of such aliens in a mound, but not sharing galleries with their host or each other.

Other animals also make use of termitaria. The fat-tailed antechinus, *Pseudantechinus macdonnellensis*, sometimes lives in *Nasutitermes triodiae* mounds. Various birds excavate nests in arboreal and terrestrial termitaria, including kingfishers and three of Australia's endangered parrots, species of *Psephotus*. The monitor lizard *Varanus varius* often lays its eggs in mounds of *Nasutitermes exitiosus* and *Coptotermes lacteus*, and pythons of the genus *Bothrochilus*, predatory on the termitophilous gecko *Gehyra pilbara*, occur in nests of *N. triodiae*.

Termitophiles. Termite nests harbour a rich fauna of other arthropods, including insects and mites (Kistner 1979, 1982). Some of these termitophiles are active predators feeding on eggs and young brood, some are merely scavengers feeding on nest debris, but many show a more intimate association with their hosts by providing attractive secretions in return for which they receive food.

These last frequently show considerable structural adaptations, such as physogastry leading, in some cases, to mimicry (Figs 35.25F, G), and highly developed excretory organs, associated with this trophallactic exchange. Termitophilic hexapods recorded from Australia include Collembola, atelurine Thysanura (p. 278), several families of Coleoptera (particularly Brentidae, Carabidae, Ceratocanthidae, Pselaphidae, Scarabaeidae, Staphylinidae and Tenebrionidae), Hymenoptera (Diapriidae) and Diptera. Perhaps the most strikingly modified are the Staphylinidae *Drepanoxenus* (Fig. 35.25E), which occurs with *Drepanotermes*, and *Austrospirachtha mimetes* (Figs 35.25F, G) and *Australoptochus phoreticus*, which occur with species of *Nasutitermes*. The larvae of *A. phoreticus* ride on their hosts (Watson and Kistner 1985).

Natural Enemies. The most important natural enemies of termites are predators of various kinds. Winged reproductives emerging on their colonising flight are eaten in large numbers by lizards, snakes, frogs, insectivorous and omnivorous birds, ants and other predatory insects, especially Odonata. Workers and soldiers of a wide range of species form an important part of the diet of the echidna (*Tachyglossus aculeatus*), which has strong, long-clawed feet with which it attacks mounds and subterranean galleries. The marsupial numbat (*Myrmecobius fasciatus*) is a specialised termite predator, and uses its strong, burrowing fore legs to open up shallow, subsurface soil galleries. Termites are significant items of food for other marsupials, including species of Dasyuridae, a bandicoot, and the bilby (*Macrotis lagotis*). Typhlopod snakes (*Ramphotyphlops*) eat termites, and are commonly found in soil under termite nests or stumps where termites are abundant. Lizards such as geckos, pygopodids and skinks also prey on termites, above and below ground, and the great abundance and diversity of lizards in arid Australia has been attributed to the abundant and diverse termite fauna there (Morton and James 1988).

Economic Significance. Termites cause many problems in Australia, but their economic cost is hard to assess (French in Vinson 1986). Only 20 or so species cause what humans regard as damage. Pre-eminent among these are *Mastotermes* and species of *Copto-*

termes, but several other genera include troublesome species (see below). Two kinds of targets suffer most of the damage, living plants and materials.

Damage to living plants involves eucalypts in indigenous forests; plantation forests and orchards; urban trees; a few crops; and pastures, native and improved. The major problem, the extensive hollowing-out of eucalypts (and occasional, similar damage in *Pinus* plantations) leads to large losses of millable timber (although it also produces the timber pipes that Aborigines use to make didgeridoos and bone coffins, and provides nest sites for many birds and mammals). However, with the exception of *Mastotermes*, termite attack appears to depend on fungal predisposition, the fungus having gained entry through fire scars or physical damage on the trunk (Perry *et al.* 1985a). The extensive, long-term denudation that *Drepanotermes perniger* has caused to pastures in South-West Qld has primarily human origins; as grass dwindled in drought, mulga removal by cutting, or overgrazing by sheep, reduced the amount of mulga litter, the termites' alternative food, and led to their destroying the residual grass tussocks.

Damage to materials is widespread, and even Aboriginal artefacts and rock art have been affected (Watson and Flood 1987). Most problems, however, involve timber and timber products in service, and various synthetic materials, principally plastics. To cope with damage to timber in service (as in buildings), two main approaches have been followed in Australia (Hadlington 1987): the use of insecticidal soil treatments under the building, to prevent subterranean termites gaining access (Lenz *et al.* 1988b, 1990); and destruction of the colony from which the termites come, either physically or by the use of slow-acting toxins that termites treated away from the nest will take back to it. Timbers, particularly for outdoor use, are commonly treated with wood preservatives. Fumigation is effective against termites that can nest in isolated pieces of timber above the ground, such as the kalotermitids, particularly *Cryptotermes*.

The most important plastics damaged by termites are cable sheaths and pipes or pipe-coatings. Usefully resistant materials, such as nylon-12, widely used as a protective jacket on cables, are hard enough and tough enough to withstand termites (Watson *et al.* 1984).

On the other hand, termites play a role in recycling dead woody materials in much of Australia, and contribute to soil formation and turnover. They store faecal residues in the soil and in their nests. Although these organic residues may not be readily available to micro-organisms, and their turnover may therefore be slow, plant roots often invade them, and they serve as a source of food for other termites. Erosion of mounds (and dissemination of their contents) can be rapid (Bonell *et al.* 1986), although it is not always so (Watson *et al.* 1988). Termites, particularly *Mastotermes*, *Porotermes* and species of *Coptotermes*, pack the tree-trunks they have hollowed with faecal material and soil, but the significance of this activity for the tree, or for turnover of organic materials, is unknown. The role of termite galleries, which are ubiquitous in most Australian soils, in aiding

penetration of soil by water is debatable, but termites can affect soil profiles and locally enrich soil nutrients (Lee and Wood 1971; Coventry *et al.* 1988). Holt *et al.* (1980) have claimed that topsoils in parts of northern Qld may be the result of termite activity during the last 8000 years, but the effects of climate on termite distributions also need to be considered.

Special Features of the Australian Fauna

The Australian termite fauna includes one endemic family, the Mastotermitidae, but in other families except the Termitidae the level of generic endemism is low. The 41 genera comprise 25 termitids, 8 kalotermitids, 5 rhinotermitids, 2 termopsids and *Mastotermes*. The termitid genera belong overwhelmingly to 1 of 3 highly endemic groups. Two are structurally specialised: the *Termes* complex, with soldiers having elongate, variously asymmetrical snapping mandibles (13 genera, 11 not known outside Australia) (L. R. Miller 1991), and the Nasutitermitinae, with nasute soldiers (6 genera, 5 endemic). The third group, the *Amitermes* complex, includes *Amitermes*, our largest genus, with perhaps 100 species (80 included in the tally below). The other four genera are endemic, apparently derived from *Amitermes*. *Invasitermes* lacks soldiers, only the second termitine genus known to do so (L. R. Miller 1984a), but it appears we may have a significant, unrecognised fauna of small, soldierless, *Amitermes*-like species.

At least three exotic species, all *Cryptotermes*, have become established in Australia. On the other hand, several Australian species have been spread to other countries, apparently in poles and sawn timber: *Mastotermes* to New Guinea, and others to New Zealand (Bain and Jenkin 1983).

The most distinctive feature of the fauna is the presence of relict primitive genera in the Mastotermitidae and Termopsidae. *Mastotermes darwiniensis*, in some ways the most primitive living termite, is the only surviving member of a family that is represented in other continents by fossil species from Tertiary deposits. The two termopsid genera survive from Gondwana. *Stolotermes*, with three mainland species and one in Tas., is represented elsewhere by two species in New Zealand and one in South Africa, and *Porotermes* has one species in south-eastern Australia, one in Chile, and one in South Africa (Calaby and Gay in Keast *et al.* 1959). Notable absences from the fauna are the Hodotermitidae (to which the endemic termitine harvesters *Drepanotermes* show many convergent similarities) and fungus-growing termites (Macrotermitinae), of major economic importance in Africa and Asia.

Two aspects of termite distribution within Australia are of special interest. The first is the paucity of species in rainforest areas. This is in marked contrast to the extremely rich termite faunas of other tropical rainforests, such as the Congo and Guyana. The second feature is the absence of some species of termites from certain types of soil. The black earths of inland north-eastern Australia are almost devoid of termites, although adjacent sandy-desert steppe soils have an abundant fauna. It is thought that the

physical characteristics of the heavy soils, which crack deeply and widely in dry conditions and become water-logged after rain, do not favour termite survival. *Mastotermes darwiniensis*, which is widely distributed

across tropical Australia, is absent from rainforest and soils which once carried rainforest (Ratcliffe *et al.* 1952), nor does it occur on the extensive bauxite soils of Cape York Peninsula.

CLASSIFICATION

Order ISOPTERA
(348 Australian spp.)

1. Mastotermitidae (1)

2. Kalotermitidae (46)
3. Termopsidae (5)

Hodotermitidae (0)

4. Rhinotermitidae (30)
- Serritermitidae (0)

5. Termitidae (266)

This classification is that of Grassé (1986); some authors regard the Termopsidae+Hodotermitidae as constituting one family, or place the serritermitids as a sub-family, commonly of the Rhinotermitidae. The tallies for all but the Mastotermitidae and Termopsidae are imprecise, and for the Rhinotermitidae and Termitidae highly so, for it is now clear that our understanding of some major genera is very incomplete. This is due partly to

new methods of collection, particularly for soil-dwelling termites and kalotermitids (Watson and Gay in Highley and Taylor 1983), and partly to the use of techniques new in Australian termite taxonomy—biological analyses of sympatric associations (Watson and Perry 1981; Watson in Barker and Greenslade 1982), gut structure (L. R. Miller 1984a,b, 1991), and the chemistry of cuticular hydrocarbons (Watson *et al.* 1989; Brown *et al.* 1990).

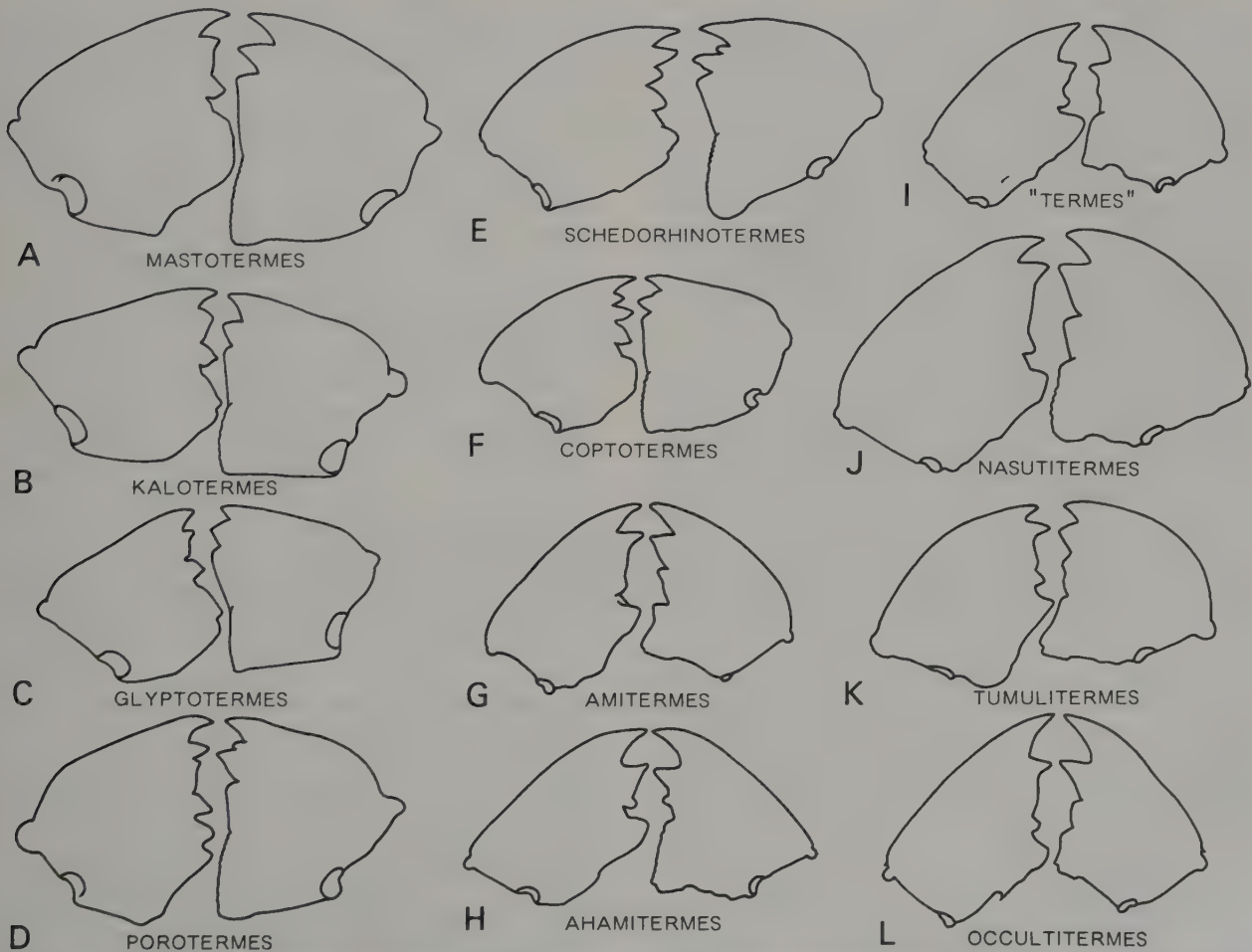


Fig. 20.14 Imago-worker mandibles in some genera of: A, Mastotermitidae; B, C, Kalotermitidae; D, Termopsidae; E, F, Rhinotermitidae; G–L, Termitidae. [N. Key]

Keys to the Families of Isoptera Known in Australia

ALATES

1. Tarsi distinctly 5-segmented, with arolium; antenna with 29–32 segments; hind wing with anal lobe ... **Mastotermitidae**
Tarsi 4-segmented, viewed from above, with or without arolium; antennae rarely with more than 22 segments; hind wing without anal lobe 2
- 2(1). Left mandible with apical and 3 well-defined marginal teeth; right mandible with small subsidiary tooth at anterior base of 1st marginal tooth (Figs 20.14D–F) 3
Left mandible with apical and 2 more or less well-defined marginal teeth, often with a long cutting edge between them; right mandible without subsidiary tooth between apical and 1st marginal tooth (Figs 20.14G–L) 4
- 3(2). Ocelli absent **Termopsidae**
Ocelli present **Rhinotermitidae**
- 4(2). Fore wing scale more than twice length of hind wing scale; wings reticulate **Kalotermitidae**
Fore wing scale less than twice length of hind wing scale; wings not reticulate **Termitidae**

SOLDIERS

1. Tarsi 5-segmented **Mastotermitidae**
Tarsi 4-segmented (rarely with a rudimentary 5th segment) 2
- 2(1). Cerci long, 4- or 5-segmented **Termopsidae**
Cerci short, 2-segmented 3
- 3(2). Pronotum with well-developed, elevated, convex anterior lobe and, as a result, saddle-shaped **Termitidae**
Pronotum transversely arched to almost flat, without elevated anterior lobe, concave to slightly convex in front 4
- 4(3). Fontanelle present **Rhinotermitidae**
Fontanelle absent **Kalotermitidae**

1. Mastotermitidae. This family is represented by the relict species, *Mastotermes darwiniensis*, which was confined to tropical Australia, but is now established in New Guinea. It is the only living member of the family, and presents many primitive characters. The tarsi are 5-segmented in all castes. The alate, which is the largest of all the Australian termites, has 29–32-segmented antennae, large eyes and ocelli, and reticulate wing venation; the hind wings (Fig. 20.2) lack the basal suture, but have a distinct anal lobe, both blattoid characters. Mandibular dentition is, however, simpler than in Blattodea, Termopsidae or Rhinotermitidae, resembling that in Kalotermitidae (Figs 20.14A, D–F). The soldiers have 20–26-segmented antennae and, in mature colonies, short, stout mandibles (Fig. 20.10B). In both alates and soldiers, the fore tibiae have 3, and the mid and hind tibiae 4 apical spurs. Eggs are laid in pods (Fig. 20.8), probably homologous with the oothecae of Blattodea; this method of oviposition is found nowhere else in the Isoptera.

M. darwiniensis occurs widely in the tropical areas of Qld, N.T. and W.A. It is not a mound-builder, and normally nests in the boles of trees, in logs or stumps, or underground. Mature colonies are headed by numerous apterous neotenes, and no physogastric reproductives are known (Watson and Abbey 1989). In undisturbed conditions the colonies are usually small but, following disturbance that substantially augments food supply (and, perhaps, reduces competition), such as clearing for plantation or settlement, their size can increase rapidly to well in excess of a million individuals. This opportunism, unusual in termites, depends on the ready availability of neotenes (p. 336). *M. darwiniensis* is very destructive and, in addition to its severe and often rapid attacks on structural timber of all kinds, it causes serious damage to living trees and crop plants, and to many synthetic materials.

2. Kalotermitidae. Alates with small ocelli close to the eyes. Fontanelle absent. Antennae 11–21-segmented. Left mandible with an apical tooth, 2 distinct, almost equal marginal teeth, and a molar plate. Right mandible with 2 marginal teeth and molar plate (Figs 20.14B, C). Pronotum flat, as broad as, or broader than, head. Tarsi 4-segmented. Fore wing scale large and overlapping hind wing scale; membrane of wings reticulate. Fore wing with Sc, R and Rs sclerotised; M varying in position; 1A absent. Hind wing with Sc absent, short 1A present. Cerci short, 2-segmented. Soldiers with robust heads and well-developed mandibles. Head generally long, but phragmotic in some genera, with sculptured frontal area (Figs 20.15B–D). Eyes rudimentary, occasionally pigmented. Antennae 10–19-segmented. Mandibular dentition varied.

Neotermes (at least 2 spp.) occurs in coastal forests from Vic. to Torres Strait and across to Darwin. Soldiers are larger than those of any other Australian termite, including *Mastotermes*. *Neotermes* forms moderately large colonies, often in systems of concentric galleries, generally in the upper portions of living eucalypts; it has also been recorded from hoop pine (*Araucaria cunninghamii*) and some ornamental trees. Although *Neotermes* produces no central pipe in the trees that it attacks, the extensive gallery systems are occasionally the cause of some economic loss in timber and in power poles in the Sydney region.

Kalotermes (12 spp.) has small, darkly pigmented alates with the wing membrane densely covered with small, pimple-like, pigmented nodules; all species have an arolium. The soldiers, with the exception of *K. atratus*, have long, narrow heads (Fig. 20.15B) and strong mandibles with varied dentition. The head of *K. atratus* is phragmotic (Fig. 20.15D). All but one species are wood-dwellers, and form small colonies in exposed dead (and,

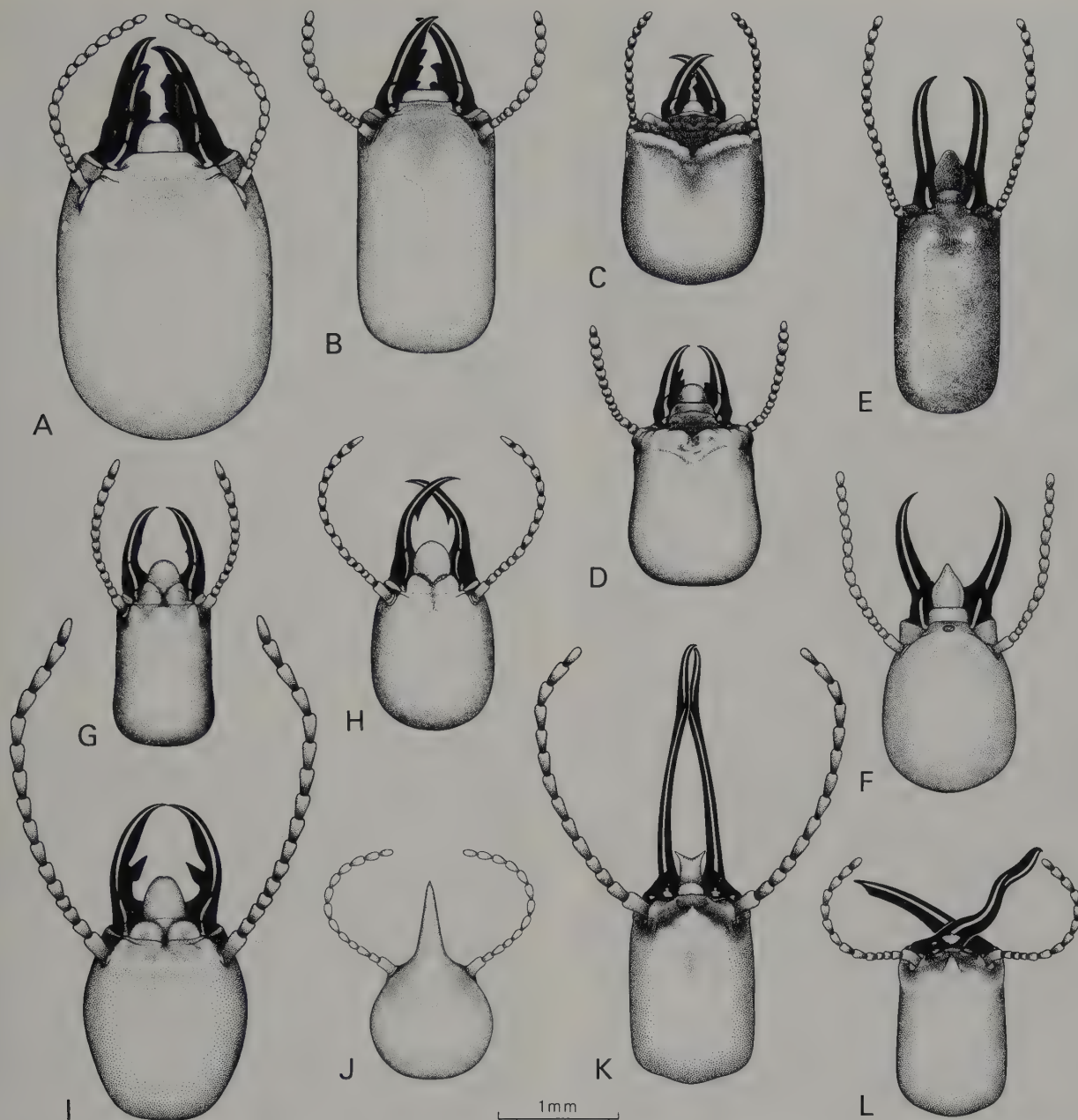


Fig. 20.15 Heads of soldiers of: A, *Porotermes adamsoni*, Termopsidae; B, *Kaloterms rufinotum*, Kalotermitidae; C, *Cryptotermes gearyi*, Kalotermitidae; D, *Kaloterms atratus*, Kalotermitidae; E, *Heterotermes intermedius*, Rhinotermitidae; F, *Coptotermes acinaciformis*, Rhinotermitidae; G, *Ahamitermes nidiicola*, Termitidae; H, *Amitermes neogermanus*, Termitidae; I, *Drepanotermes tamminensis*, Termitidae; J, *Nasutitermes carnarvonensis*, Termitidae; K, *Macrognathotermes sunteri*, Termitidae; L, *Paracapritermes primus*, Termitidae.

[B. Rankin]

commonly, decayed) wood, branch stubs and fire scars; one undescribed species nests in fibrous eucalypt bark. *K. banksiae* occasionally damages timber in buildings. Except for *K. aemulus* and *K. hilli*, which occur in south-western Australia, and *K. serrulatus* from tropical Qld, they are restricted to the coastal and adjacent highland areas of south-eastern Australia and Tas.

Incisitermes (2 spp.) has medium-sized, pale brown alates with hyaline wings and, in Australian species, an arolium. Soldiers have more or less parallel-sided, rectangular heads, short stout mandibles, the 3rd antennal seg-

ment long and clavate, and swollen femora (Gay 1976a). *I. barretti* is common in coastal North Qld, in *Acacia*, *Eucalyptus*, the mangrove *Ceriops* and, occasionally, in buildings, and an undescribed species occurs in similar habitats on Cape York Peninsula and on Torres Strait islands.

Ceratokaloterms is represented by 2 species. *C. spoliator*, the better known, occurs in coastal and adjacent highland areas from southern N.S.W. to northern Qld, and forms small colonies in and around dead wood in species of *Eucalyptus*. The alates are dark brown, with dark

brown wings and an arolium, and soldiers have narrow, parallel-sided heads with two large, anterodorsal prominences, long, slender mandibles, and a deeply V-shaped anterior pronotal margin.

Glyptotermes (6–7 spp.) has reddish brown to dark brown alates with smoky brown wings; Rs and M are both heavily sclerotised, Rs is unbranched, and M runs closely parallel to it. The soldiers have a more or less elongate head which is distinctly to faintly bilobed in the frontal area; the mandibles are short and broad. The species are restricted to the coastal and adjacent tableland areas of eastern and south-eastern Australia from North Qld to Adelaide. They form small to, occasionally, large colonies in dead wood, often decayed, and adjacent sound wood of trees belonging to several genera, and can severely damage power poles.

Bifiditermes improbus occurs in coastal areas from southern Qld to W.A. The alates have hyaline wings and lack an arolium. The soldiers have long, thick, parallel-sided heads, with the 3rd antennal segment enlarged and clavate. *B. improbus* forms small to moderate-sized colonies which occupy irregular gallery systems in decayed and sound wood of eucalypts, and occasionally in buildings (Watson *et al.* 1984), and is quite common in Sydney in eucalypt power poles with intact sapwood.

Procryptotermes (2 spp.) occurs from Central Qld to the N.T. (Gay 1976b). The alates are pale brown, morphologically like those of *Cryptotermes*, and with similar mandibles. The soldiers have relatively short, slightly phragmotic heads and long mandibles, the 3rd antennal segment is clavate, and the anterior margin of the pronotum is not serrated. Nests of *P. australiensis* and an undescribed species have been found in dead wood, principally of eucalypts.

Cryptotermes (18 spp.) is the largest kalotermitid genus in Australia. It has variously coloured alates, all with the anterior margin of the 3rd marginal tooth of the left mandible far longer than the posterior margin of the 1st+2nd tooth, and all species except *C. brevis* have an arolium. Soldiers have phragmotic heads, with frontal and/or genal horns, short or long mandibles usually humped basally (Fig. 20.15c), and the anterior margin of the pronotum variously serrate or lobed (Gay and Watson 1982). Most species are eastern or northern, usually coastal, the endemic species commonly nesting in dead tissue of eucalypts, but *C. austrinus* and *C. cristatus* occur in Central or Western Australia. An undescribed species nests in white cypress pine (*Callitris*) in northern N.S.W.; *C. brevis*, *C. cynocephalus*, *C. domesticus*, *C. dudleyi* and *C. primus* commonly establish nests in timber in buildings (Fig. 20.12b); some infest furniture. Some or all populations of the first four of these species appear to be introductions; *C. brevis* (West Indian drywood termite) is established in Central and South-East Qld, whereas the others are northern. *Cryptotermes* infestations are often indicated by dry, sand-like faecal pellets expelled from openings in their gallery systems. [Krishna 1961]

3. Termopsidae. Alates without ocelli or fontanelle. First marginal tooth of right mandible with a small subsidiary tooth on the distal edge (Fig. 20.14d). Pronotum

flat and narrower than the head. Scales of fore wing larger than those of hind wing. Tarsi 4-segmented. S9 of males with styles. These are the true damp-wood termites; all species are found in wood, principally in fungus-affected wood in standing trees or fallen logs. They can also infest damp timber in service. The family is divided into 3 subfamilies, of which 2 occur in Australia, each being represented by a single relict genus.

In the POROTERMITINAE, the alates have 5-segmented cerci, and the soldiers have long, rounded to rectangular heads, with stout, toothed mandibles about one-third the length of the head (Fig. 20.15A). *Porotermes adamsoni*, the only representative of this subfamily, occurs in coastal and adjacent highland areas from southern Qld to Tas. and S.A. It is found mainly in hardwood forests, where it forms moderately large colonies in both dead and living trees as well as in logs. Colonies in trees construct gallery systems, which may extend from the roots to the main branches, and frequently include a large central pipe which is packed with moist, clay-like, faecal material. There may possibly be connections between adjacent infestations via the soil. *Porotermes* is responsible for economic damage to commercial-timber trees (cf. Elliott and Bashford 1984), and also to poles and structural timber in moist situations in and near Melbourne, in the Blue Mountains west of Sydney and, occasionally, in Canberra (Watson 1988).

In the STOLOTERMITINAE, the alates have 4-segmented cerci, and the soldiers have markedly flattened bodies and heads, with strongly toothed mandibles that are at least half as long as the head. *Stolotermes* is represented by 4 species: 1 in Tas.; 1 in mountainous country from Vic. to southern Qld, and 2 on the Atherton Tableland and nearby montane areas in North Qld. All form small to moderate-sized colonies in rotten logs on the ground or in pockets of decay in living trees.

4. Rhinotermitidae. Alates generally with ocelli (sometimes absent in *Heterotermes*). Fontanelle present, sometimes indistinct. Antennae 14–22-segmented. Left mandible with 1 apical and 3 marginal teeth; right mandible with a small subsidiary tooth at base of the 1st marginal (Figs 20.14E, F). Pronotum more or less flattened. Tarsi 4-segmented. Scale of fore wing large; wings often reticulate. Cerci 2-segmented. Soldiers various, generally without eyes. Mandibles well-developed, with or without marginal teeth. Fontanelle present. Antennae 12–18-segmented. Pronotum flattened. Almost all species are wood-eaters and all are subterranean in habit, although some construct conspicuous mounds. Four of the 7 subfamilies occur in Australia.

In the HETEROTERMITINAE, the alates have elongate-oval heads with flattened sides, and the wing membrane is slightly reticulate. The soldiers have long, rectangular heads, with sabre-like mandibles devoid of obvious marginal teeth (Fig. 20.15E). *Heterotermes* (perhaps 12 spp.) are all small, and are widely distributed throughout mainland Australia in both coastal and inland areas. Their taxonomy is not clearly understood (Watson *et al.* 1989). The colonies are usually small, and are found in the soil, in or under logs and stumps, in dieback wood, and in the

mounds of other species of termite. All species are wood-eaters, commonly weathered wood, and some are of economic importance.

In the COPTOTERMITINAE, the alates have heads circular in plan, a small clypeus, a relatively broad pronotum, and the wing membrane is not reticulate. The soldiers have pyriform heads with a conspicuous fontanelle, and sabre-shaped mandibles without obvious marginal teeth (Fig. 20.15F). *Coptotermes* (10 or more spp.) is widely distributed throughout the mainland, and readily recognised by the soldiers' habit of exuding a drop of milky fluid from the frontal gland when disturbed. All species appear to form large colonies, which may exceed a million individuals. The nests are subterranean, or in stumps or hollowed trunks of dead or living trees, or in domed or conical mounds up to 3 m high. This mound-building habit is unusual in *Coptotermes* for, although the genus is widespread in the warmer regions of the world, it builds mounds only in Australia. The mounds (Fig. 20.12G) are characterised by a clay outer wall up to 30 cm thick, enclosing a woody, often tough interior. All species are wood-eaters, and some cause severe damage to timber in service, to living trees, and to synthetic materials. They constitute the most important economic group of termites in Australia but, as with *Heterotermes*, their taxonomy is poorly understood (Brown *et al.* 1990). *C. acinaciformis*, which appears to include more than 1 species, occurs in all States, but is a mound-builder only in the northern and south-western portions of its range. *C. frenchi*, also a species complex, is restricted to eastern and southern Australia, and builds mounds only in the south. *C. michaelsoni* in south-western Australia does not build mounds. Other species are less important economically. *C. lacteus* from south-eastern Australia and *C. brunneus* from W.A. are obligate mound-builders; the mounds of *C. brunneus* conserve water (Watson in Howes 1978).

The subfamily PRORHINOTERMITINAE includes only the genus *Protermitermes*. The alates have heads nearly circular in plan; clypeus swollen, grooved medially; 2nd marginal tooth of left mandible much larger than 1st; and wings strongly reticulate. Soldiers have elongate, sabre-like mandibles and a small, distinct fontanelle, linked to the clypeus by a gutter, but lack a labral brush. The nymphal wing buds are fused in the midline, forming cowl-like structures. *P. inopinatus*, widespread in the south-western Pacific, occurs on Cape York Peninsula and in the N.T. (Gay and Barrett 1983).

The RHINOTERMITINAE are characterised by alates with heads circular in plan; clypeus well developed and inflated, with a distinct median groove from the fontanelle to the labrum; and wings with distinct reticulation. The soldiers have an elongate, medially grooved labrum, conspicuous fontanelle, and well-developed mandibles with large marginal teeth. *Schedorhinotermes* (6 spp.) is unusual in possessing two or three distinct types of soldiers, differing in size and in the shape of heads and mandibles (Figs 20.10E, F) (L. R. Miller 1987). Colonies are small to moderate in size, and are located in stumps, in and under logs, or in the soil. Frequently the attack on posts, logs, bark or dead branches is carried out under the

protection of fragile, roof-like plastering, but *S. derosus*, a harvester, gathers grass in the open, 50 cm or more from shelter (Watson 1969b). *Parrhinotermes* is represented by a single species, *P. queenslandicus*, found only in moist decayed logs in rainforests in North Qld.

5. Termitidae. Alates with ocelli, and usually with a fontanelle (vestigial or absent in *Microcerotermes*). Antennae 13–18-segmented. Mandibular dentition various (Figs 20.14G–L). Tarsi 4-segmented. Fore wing scale about as large as, or only slightly larger than, hind wing scale. M closer to Cu than to Rs. Soldiers either with rounded or rectangular heads bearing obvious mandibles with or without teeth, or with nasute-type head and vestigial mandibles. Antennae 10–20-segmented. Pronotum saddle-shaped. Workers with 12–19 antennal segments. Postclypeus generally inflated. Pronotum saddle-shaped.

This is the largest family in the order. It is divided into 4 subfamilies. Fungus-growing termites (Macrotermittinae), prominent in Africa and Asia, do not occur in Australia, nor do Apicotermitinae. Many Australian termitids eat wood or grass, but some are detritivores; others consume soil for the humic material it contains, or subsist on organic material in the fabric of other termites' nests. Subterranean nests are common, but many species build mounds, and a few construct arboreal nests.

In the TERMITINAE the soldiers have well-developed mandibles, and a fontanelle more or less flush with the surface of the head. Two groups can be recognised, the *Amitermes* group in which the soldier mandibles are specialised for biting, and the *Termes* complex, in which the mandibles have a snapping action.

The *Amitermes* group includes 6 Australian genera. *Amitermes*, almost cosmopolitan, is our largest (Gay 1968), with perhaps 100 species. Soldiers, which are often infrequent, have a single tooth—barbed, peg-like or hatchet-shaped—on each mandible, which is usually incurved (Fig. 20.15H). Species of *Amitermes* are most abundant in the inland areas of northern and western Australia, and in Central Australia. Most are subterranean, but several build mounds, the best-known being the meridional mounds of *A. laurensis* and *A. meridionalis* in Cape York and the N.T. (Figs 20.12E, H). An undescribed species builds arboreal nests in the same regions. The diet is usually plant detritus or grass, but some species consume dung and others, weathered wood.

Drepanotermes (23 spp.) is an endemic genus of harvesters derived from *Amitermes* (Watson and Perry 1981). These Australian harvester termites parallel in many ways the African hodotermitid harvesters *Hodotermes* and *Microhodotermes*. The soldiers have long, sickle-shaped mandibles, usually with a prominent tooth, larger on the left mandible than on the right (Fig. 20.15I), and both soldiers and workers commonly have orange, reddish brown or black heads and dark bodies. Seven of the species sometimes or always build mounds, usually low, but those of *D. columellaris* rise to 2 m; several species take over mounds of other termites, including *Nasutitermes triodiae*. The mounds can be very long lived, and each colony may occupy more than one mound (Watson *et al.* 1988). *Drepanotermes* occurs in the drier areas of all

mainland states, but the greatest concentration of species is in north-western Australia. The diet is primarily dry grasses and forbs, leaf litter and twigs, which the termites usually cut into pieces about 1 cm long and store in their nests. Some species, particularly *D. perniger*, have been implicated in pasture denudation, but this appears to be primarily a problem of range management.

The endemic *Ahamitermes* (3 spp.) and its more specialised derivative *Incolitermes* (1 sp.) are obligate inhabitants of *Coptotermes* nests, where they eat nest material. The apical teeth are enlarged in the imago-worker mandibles, and the marginal teeth are compressed (Fig. 20.14H). The soldiers have short, stout mandibles with vestigial or no teeth (Fig. 20.15G). The nests of *I. pumilus* are completely surrounded by those of its host, and it cannot release its own alates, depending instead on the host workers when they release theirs.

Invasitermes (2 spp.) are soldierless inquiline in the nests of *Nasutitermes* and *Amitermes*, commonly *A. laurensis*. The imago-worker mandibles have enlarged apical teeth, widely separated from the 1st marginal teeth (as in *Ahamitermes*, *Incolitermes* and some species of the *Termes* complex); indeed, alates of both species, *I. inermis* and *I. insitivus*, were originally placed in that complex, *I. inermis* as the alate of *Lophotermes quadratus* (L. R. Miller 1984a). Mandibular similarity appears to be convergent, linked to soil feeding.

Microcerotermes (16 spp.) is found all over the continent except in the south-eastern corner, and is much in need of taxonomic revision. The fontanelle is indistinct or wanting in the alates, and the soldiers have long, rectangular heads, with long slender mandibles which are generally obviously serrate on their inner margins (Fig. 20.10D). All species are wood-eaters and most are subterranean, but five species regularly build small, conical or domed mounds on either the ground, stumps, logs or the trunks of dead and living trees. Several species occasionally damage timber in service, and *M. serratus* has severely damaged railway sleepers in north-western Australia.

In the *Termes* complex, revised by L. R. Miller (1991), the alate-worker mandibles usually have the apical tooth much larger than the 1st marginals, and separated from them by a long gap (Fig. 20.14I), as in other soil-feeding termites. The soldiers are equipped with long, slender, curved mandibles, variously asymmetrical (Figs 20.15K, L), which can store energy when closed under tension, releasing it in a snapping action. Soldiers of most species have a frontal tubercle extending above the fontanelle, and may also have lateral tubercles beside the frontal tubercle. The group is best developed in northern Australia.

In the more generalised forms, the asymmetry in the soldier mandibles is limited to greater curvature of the left mandible (Fig. 20.15K). Such forms, previously included in *Termes* (Gay 1971), are now known to belong to 10 different genera, distinguished primarily on gut structure and mandibular dentition: *Apseotermitermes* (5 spp.), *Cristatitermes* (6 spp.), *Ekphysotermes* (5 spp.), *Ephelotermes* (6 spp.), *Hapsidotermes* (5 spp.),

Hesperotermes infrequens, *Lophotermes* (9 spp.), *Macrognathotermes* (4 spp.), *Saxatitermes saxatilis* and *Xylochomitermes* (6 spp.). All are endemic, and all but *Ephelotermes*, *Hesperotermes* and *Xylochomitermes* feed on soils (35 species altogether, the largest group of Australian soil-feeders). The remainder mostly eat weathered or partly decayed wood, although *Ephelotermes cheeli* may attack relatively sound timber. A few species build mounds or arboreal nests, but most are subterranean, or nest in mounds of other termites (L. R. Miller 1991).

Soldiers of *Protocapritermes krisiformis*, *Paracapritermes* (4 spp.), and an undetermined species of *Pericapritermes* (the first two genera endemic) have flattened and kinked left mandibles (Fig. 20.15L), particularly in *Pericapritermes*. *Protocapritermes* lacks a frontal tubercle, and eats soil; the others feed on weathered or decayed wood. *P. krisiformis* builds small, blackish mounds only a few cm high, in coastal N.S.W. and southern Qld.

Soldiers of Australian NASUTITERMITINAE have pyriform heads and greatly reduced mandibles, and the fontanelle opens at the end of a distinct frontal tube traversing the rostrum (Figs 20.10G, H, 15J). On the left imago-worker mandible the apical and 1st marginal teeth are almost equal in size and the 2nd marginal is developed into a long, blade-like structure (Figs 20.14J, K), except in soil-feeding genera, which have a *Termes*-like configuration (Fig. 20.14L).

Nasutitermes (perhaps 30 spp., 19 described) is widely distributed throughout Australia, particularly in the northern half of the continent. The soldiers are of the typical nasute type, generally of only one size, and the head is without an evident constriction when viewed from above (Fig. 20.15J). The genus includes subterranean species, many undescribed, as well as some that build mounds or tree-nests, and form colonies of 1–2 million individuals. Food materials include grass, vegetable debris, rotten and sound wood, but generally not coniferous timbers. *N. graveolus*, which occurs in coastal and near coastal districts from Mackay to Darwin, including Torres Strait islands, and *N. walkeri* in similar districts and some inland areas from south of Sydney to Cairns both construct dark, rounded nests on the trunks and branches of dead and living trees (Fig. 20.12F); they feed mainly on bark and weathered wood, but *N. graveolus* sometimes causes severe damage to timber in service. *N. magnus* is a grass-eating species which occurs commonly in coastal and near coastal districts from Grafton to Cairns, and has also been found in Central Australia. It builds low, domed mounds, up to 2 m in basal diameter and 1 m in height, which are usually stocked with abundant chaffed grass. *N. triodiae*, a grass-eater found in northern Qld, the N.T. and north-western Australia, constructs large mounds of varying types, the most spectacular being massive columnar structures more than 7 m high (Fig. 20.12I). These huge nests are unique for the genus, which has a wide distribution in the warmer regions of the world. *N. exitiosus*, which extends from just north of the Qld–N.S.W. border, through Vic. and S.A., across to W.A., is of considerable economic importance because of the damage it causes to

timber in service. Throughout the more coastal parts of its range it builds low, dome-shaped mounds, about 1 m in basal diameter and 50 cm high (Fig. 20.13), but inland it can be completely subterranean.

In *Tumulitermes* (perhaps 50 spp., 18 described), the soldier has a relatively long, slender rostrum, and the head is often markedly constricted behind the antennae (Fig. 20.10H). Several species have two distinct classes of soldier which differ in size and, occasionally, in structure (Figs 20.10G, H). This endemic genus, which may be a complex, is widely distributed throughout Australia with the exception of the south-eastern region, and is most abundant in the arid and semi-arid areas. Most species are completely subterranean, but at least five are known to construct mounds, and many invade mounds of other termites. They all appear to be surface foragers, and their nests are stocked with stores of grass and other vegetable matter, sometimes processed into pellets. *T. hastilis* builds tall narrow mounds up to 2 m high in inland Qld, the N.T. and W.A. In some districts these mounds are so numerous as to constitute a distinctive feature of the landscape.

The remaining Australian genera in this subfamily are also endemic. In *Occasitermes* (2 spp.) the soldiers are rarely dimorphic, the soldier head is not constricted, and the rostrum is long, conical and thick at the base. *O. occasus* is common in south-western W.A. and has been

recorded from S.A., and *O. watsoni* is known only from inland N.S.W. (Gay 1974). Both are subterranean, feeding on rotted or weathered wood or bark. *Occultitermes* (2 spp.) also shows rare soldier dimorphism, the head is unconstricted, and the rostrum is long, slender and almost cylindrical. *O. occultus* is known only from Cape York Peninsula, the Top End of the N.T. and the far north of W.A., whereas *O. aridus* extends to southern inland Qld and central W.A. (Gay 1977). Both are probably detritivores, and are subterranean.

Australitermes (3 spp.) and *Macrosbulitermes greavesi* are not closely related to the other nasute genera, differing from them in gut structure (L. R. Miller 1984b). They are closely allied soil-feeders, and the imago-worker mandibles have elongate apical and reduced marginal teeth and a smooth, rounded molar plate. The soldiers are monomorphic, and their heads are broad and rounded; the rostrum is long and slender. All are confined to the far north except *A. dilucidus*, which extends into south-eastern Qld. *A. insignitus* was earlier placed in *Termes*, and *A. perlevis* in *Macrosbulitermes*.

ACKNOWLEDGMENTS. We thank Professor E. A. McMahan, Mr J. W. Creffield and Mr R. H. Eldridge for their helpful reviews of the manuscript, Mr Eldridge for providing Fig. 20.12F, and Mr L. R. Miller for the draft of Fig. 20.7.

Mantodea*

(Praying mantids)

J. BALDERSON

Mandibulate, predacious, exopterygote Neoptera; head freely mobile; antennae multisegmented and usually fili-form; fore legs raptorial with large mobile coxae; mid and hind legs cursorial; tarsi almost always 5-segmented; fore wings modified into hardened tegmina, hind wings membranous; tegmina and wings may be fully developed, shortened or (particularly in females) absent; specialised auditory organ on metathorax; cerci multisegmented; male genitalia strongly asymmetrical; eggs enclosed in an ootheca.

Mantids are predominantly rather large and slender terrestrial insects. They are found in all the warmer parts of the world but show their greatest diversity in the tropics. Some 1800 species are known. The name mantis is derived from the Greek for seer or prophet, probably an allusion to its apparently praying stance. Mantids appear in the mythology and folklore of many cultures from the ancient Egyptians to present times. The fossil record, although sparse, is sufficient to indicate a common Palaeozoic ancestry with the Blattodea. Although originally classified as a family in the order Orthoptera, or combined, for example, with the Blattodea in the Dictyoptera (Richards and Davies 1977), the Mantodea is now more generally regarded as a separate order (see also Kevan 1977a for full discussion).

General accounts of the order are given by Chopard (1949a) and Beier (1964).

Anatomy of Adult

Head. Freely movable on a slender neck and rarely inserted to any extent into the pronotum; typically hypognathous, flattened anteroposteriorly, subtriangular, the large compound eyes occupying the dorsolateral corners

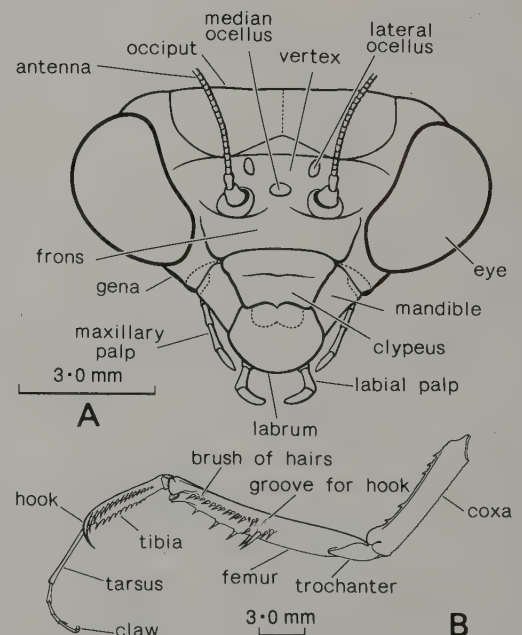


Fig. 21.1 *Archimantis latistylus*, Mantidae, ♀: A, head, face view; B, right fore leg, ventrocephalic (ventrointernal) view. [F. Nanninga]

* Some parts of this chapter are from Key (1970).

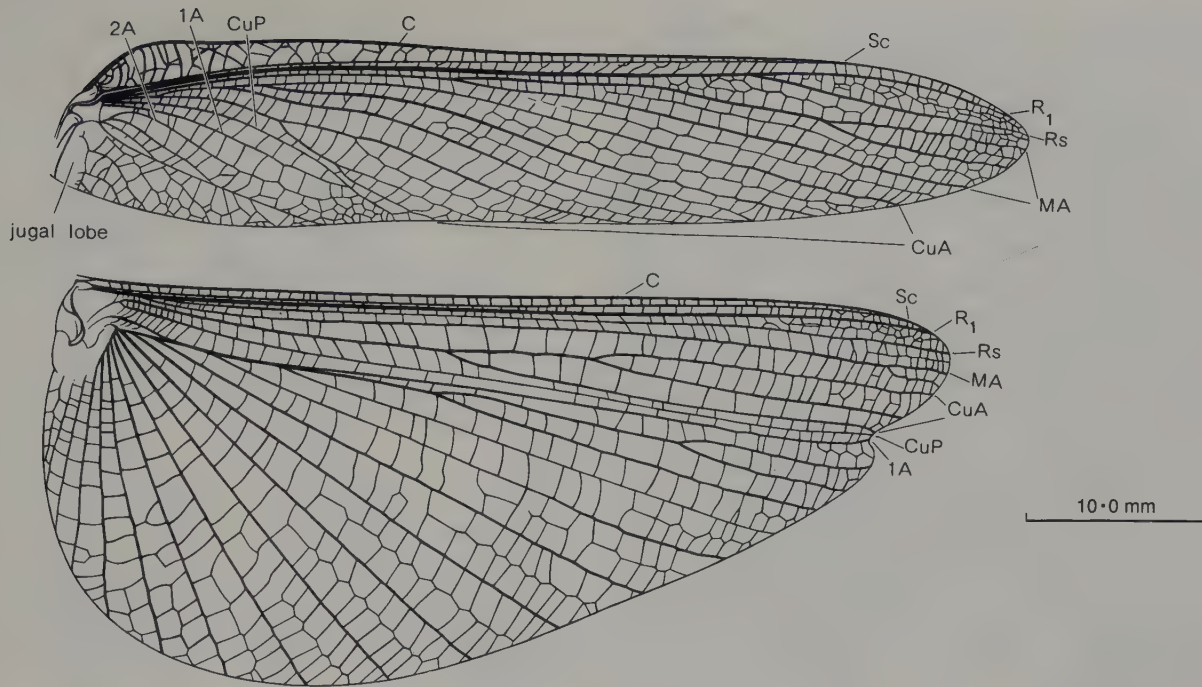


Fig. 21.2 *Archimantis latistylus*, Mantidae: wings of ♂.

[F. Nanninga]

and the narrow mouth the ventral apex (Fig. 21.1A). Frontal shield well-defined, taxonomically significant. Eyes usually rounded but sometimes conical or pointed. Antennae slender, many-segmented, ciliate, longer in male than female; Johnston's organ in pedicel; flagellum with a large number of chemoreceptors but no tactile hairs (Slifer 1968). Ocelli three, larger in the male than in the female. Mouth-parts almost covered by mobile labrum; comprising strong, slightly asymmetrical, toothed mandibles; maxilla with 5-segmented palp, soft galea, and toothed lacinia; and labium with 3-segmented palps and well-developed glossae and paraglossae. Hypopharynx large.

Thorax. Prothorax usually narrow and elongate, movable on the mesothorax; pronotum transversely arched, sometimes with leaf- or shield-shaped lateral expansions, but without descending lateral lobes, not produced posteriorly over the wing bases; prosternum sclerotised, with short basisternum and long sternellum; propleura greatly reduced, the pronotum for most of its length connecting directly with the sternum. Meso- and metathorax similar, not elongated, rigidly connected; the sterna largely sclerotised, with large basisternum and small sternellum; pleura oblique, the epimera very narrow. Meso- and metathoracic spiracles present. Specialised auditory structure in ventral midline between metathoracic legs, responsive primarily to ultrasound between 25 and 45kHz (Yager and Hoy 1986).

Legs. Mid and hind legs cursorial, slender and unspecialised, with large coxae usually closely approximated ventrally. Fore legs (Fig. 21.1B) raptorial; coxae elongate and mobile; femora robust, with a row of inner and outer spines ventrally and 3 or 4 proximal discoidal spines,

often with conspicuous colour markings on inner face, and with a brush of short hairs distally on the inner face; tibiae in all Australian species with 1 or 2 rows of ventral spines and a strong, sharp terminal claw on the inner margin; when the tibia is flexed against the femur, the spines enmesh and the claw fits into a groove on the inner face of the femur. Tarsi of all legs slender, almost always 5-segmented, with a pair of terminal claws but no arolium, those of the fore legs articulated to the tibia laterally before the apex in Australian species.

Wings. In the male usually fully functional (Fig. 21.2); in the female of most Australian species reduced or absent. Fore wings narrow, usually tougher, tegminised, and more opaque than the hind wings, in the closed position overlying them along the abdomen, the one broadly overlapping its fellow except at the extreme base, and each with a small jugal lobe, which is folded under when the wings are closed. Hind wings much broader, membranous, except often for a narrow zone along the anterior margin, with a large anal area folding fanwise in repose. Venation (Ragge 1955a) with C strongly developed along the whole anterior margin of both wings; Sc unbranched; R situated close behind Sc, divided near the base in the hind wing, and usually, but more distally, in the fore wing, into R_1 and R_s , which in the hind wing run parallel and unbranched to the wing apex; MA just behind R and branched or unbranched; CuA branched, CuP unbranched; several anals in the fore wing and many in the hind; often with a pronounced stigma between MA and CuA on the fore wing.

Abdomen. Dorsoventrally compressed, consisting of 11 segments. T10 constitutes the supra-anal plate. S1 reduced and usually not recognisable; S11 represented by

the paraprocts. Cerci segmented. Spiracles situated in the pleural membrane of T1 and on the ventral borders of T2–8. In the male (Snodgrass 1937), S9 is the subgenital plate, usually spoon-shaped (Fig. 21.3A); it usually bears a pair of styles and partly conceals the genitalia, which comprise a complex, strongly asymmetrical set of 3 partly sclerotised lobate phallomeres which bear a number of processes of considerable taxonomic value (Fig. 21.3C) (La Greca 1954); S10 is reduced and internal. In the female, S7 is the subgenital plate (Fig. 21.3B); it narrows and divides posteriorly, enveloping the ovipositor, which consists of three pairs of small valves (Marks and Lawson 1962); S8–10 reduced and internal.

Internal Anatomy. The tracheal system is primitive, holopneustic, and has no specialisations. The alimentary canal is relatively straight, with a large crop, conical gizzard with 6 internal teeth (Judd 1948), and short mid gut bearing 8 caeca; complex, paired salivary glands lie along the gut, and there are about 100 Malpighian tubules. The central nervous system includes 3 thoracic and 7 abdominal ganglia. The male reproductive system consists of large paired testes opening into the ejaculatory duct, to which are connected paired vesiculae seminales and a mass of tubular accessory glands, whose secretions are involved in the formation of the spermatophore. In the female, ovaries composed of numerous panoistic ovarioles discharge into a common oviduct; the spermatheca and the voluminous accessory glands, whose secretions form the ootheca, open independently into the genital atrium.

Karyotype. The Mantodea have a chromosome set with $2n\delta$ ranging from 15 to 39 in the species studied (M. J. D. White 1965), all or most of the chromosomes being usually metacentric. The male is usually XO, but in many genera there is an X_1X_2Y sex mechanism.

The cytology of about 10% of Australian species has been investigated (see M. J. D. White 1976). The few Paraoxypilinae studied have an XO sex determining mechanism with $2n\delta = 25$. Within the Mantidae the subfamilies Orthoderinae and Mantinae have X_1X_2Y sex determining mechanisms with $2n\delta = 25$ in Orthoderinae and $2n\delta = 27$ in Mantinae. In the Iridopteryginae *Ima fusca* has a unique XY sex determining mechanism with $2n\delta = 34$. Other Iridopteryginae have an XO mechanism with $2n\delta = 25$.

Immature Stages

The egg is cylindrical and thin shelled. Upon hatching, the young make their way out of the ootheca (Fig. 21.4) via the mid-dorsal apertures. Each is enclosed in the embryonic cuticle, which bears minute, backwardly-directed spines on the dorsal surface and a dark, strongly sclerotised, spindle-shaped plate anteriorly; the appendages are held against the body, pointing backwards. Immediately after emergence, while the hind end is still lodged in one of the apertures—or, in some species, while suspended from the ootheca by silken threads—the insect casts the embryonic cuticle and the appendages can be moved freely. This brief first stage has been termed the ‘pronymph’, or ‘vermiform larva’, and the ecdysis by

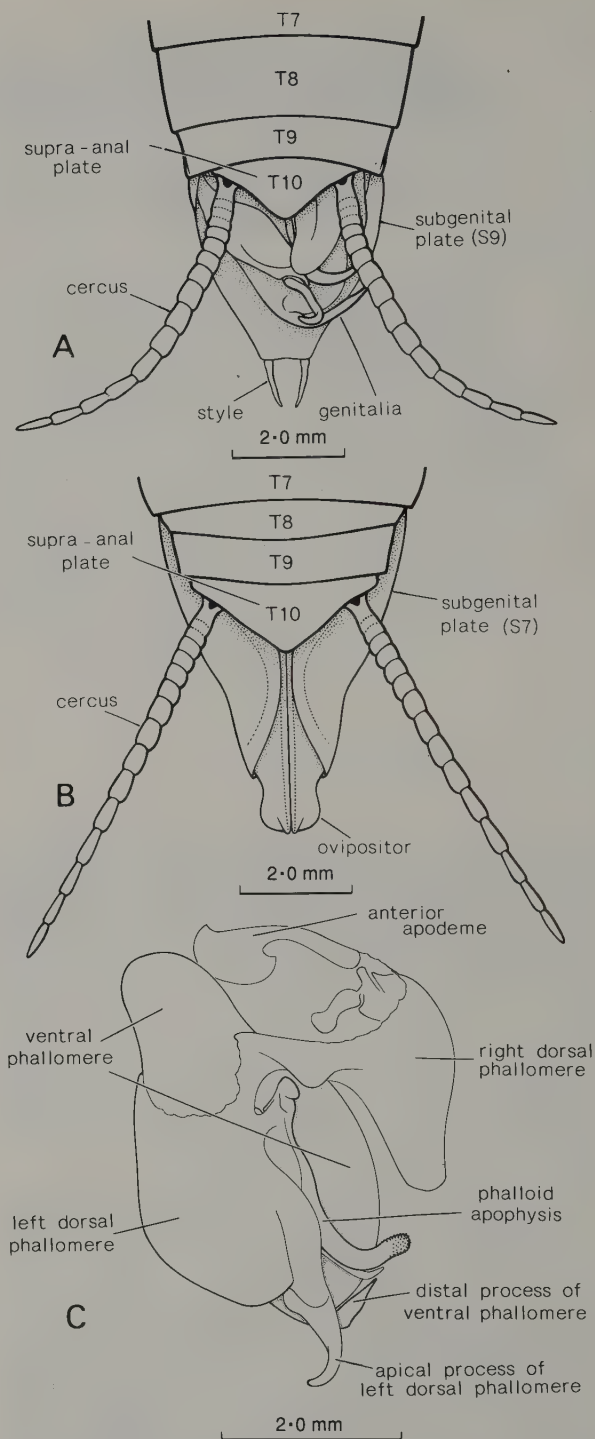


Fig. 21.3 *Tenodera australasiae*, Mantidae, dorsal views: A, ♂ terminalia; B, ♀ terminalia; C, ♂ genitalia. [A, B by F. Nanninga; C by G. Milledge]

which it is terminated the ‘intermediate moult’; it is not regarded as one of the nymphal instars.*

The nymphs (Fig. 21.5) show only minor morphological differences from adults, involving principally the rudi-

* The term ‘instar’ is used in this chapter in the conventional sense of a developmental stage delimited by ecdysis, which in turn is treated as the final and definitive episode of the moult.

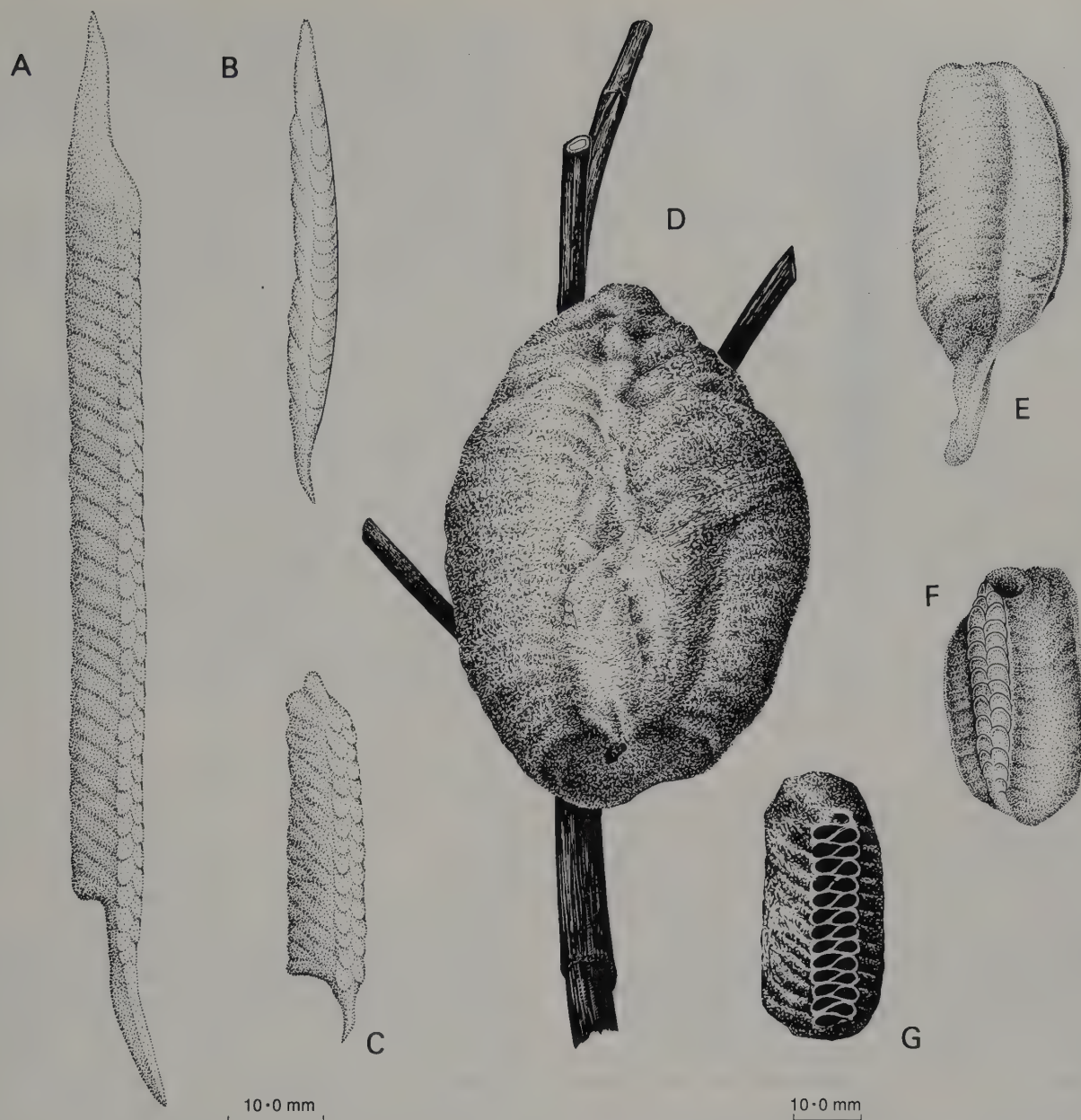


Fig. 21.4 Oothecae of Australian Mantodea: A, *Gyromantis kraussii*; B, *Kongobatha diademata*; C, *Paraoxypilus tasmaniensis*; D, *Archimantis latistylus*; E, *Mantis octospilota*; F, *Pseudomantis albofimbriata*; G, *Orthodera ministralis*. [A–C, E, F by G. Milledge; D, G by F. Nanninga]

mentary wings, immature terminalia, and lower number of antennal segments. They pass through several ecdyses (usually fewer in the male than in the female), which take place in an inverted position from some support. The wing rudiments and terminalia increase in size from instar to instar. All prematuration divisions are usually completed in the testis by the time of the last ecdysis. The life cycle is usually univoltine in cooler parts of Australia, the winter being spent in egg diapause but overlapping of generations frequently occurs in warmer regions.

Biology

Information on the biology of the order can be found in Chopard (1938).

Adults. Mantids are found in virtually any habitat which will enable them to exploit prey reserves. These range from tree canopies to shrubs (whether in flower or not), tree trunks, tall grasses or on the ground. Individuals tend to be widely dispersed and solitary. Territorial behaviour has been suggested for a number of species that use visual cues, such as displaying colour markings on the inner face of the fore legs. The 'boxing' display shown by a number of species may also be a means of spacing out the species.

Mantids are strictly carnivorous and feed mainly on insects but some of the larger species have been recorded feeding on frogs, small lizards and even fledgling birds. Many species spend much of their time standing with the

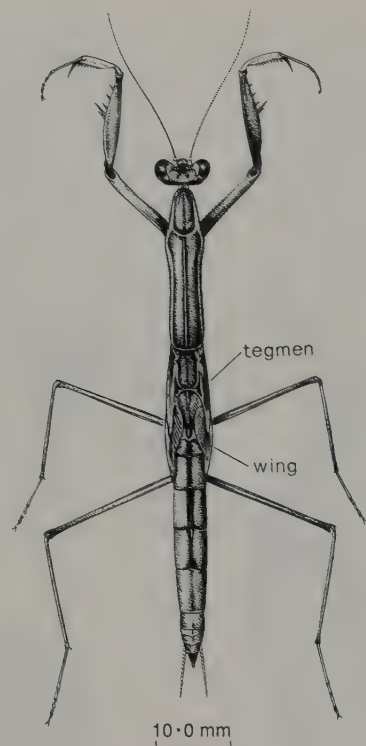


Fig. 21.5 *Tenodera australasiae*, Mantidae: late nymph. [F. Nanninga]

fore legs raised in a 'prayer-like' attitude awaiting prey. Some long-legged species sway gently from side to side; this may assist in stalking prey undetected or cause a predator to mistake them for a twig swaying in the wind. Although some ground and tree trunk dwelling species are known to actively pursue their prey, most rely on their cryptic coloration and immobile stance to enable them to wait undetected until the prey is within catching distance. Once the prey is within range the fore legs are shot forward and it is caught, impaled and held fast between the spines lining the femur and tibia. The leg is then retracted and brought up to the mouth-parts where the prey is eaten at leisure.

Reproduction. Little courtship behaviour has been observed in the Mantodea although recent studies on one species have found that it is more complex than earlier workers believed (Liske and Davis 1987). It is known that sex attractant pheromones are used by females of at least one species (Robinson and Robinson 1979). Reproductive behaviour consists in general of the male leaping onto the back of the female at an opportune moment. He then positions himself so as to clasp the female's mesothorax and the upper edge of the tegmina with his fore legs. The abdomen is lowered to the side and the end is curved sharply so that the phallic organs are directed forward and into the female genital chamber. Copulation usually lasts at least half an hour but may take much longer and culminates in the transferring of a small spermatophore to the female. Cannibalism of the male by the female has been observed frequently under caged conditions particularly when insufficient food has been supplied, but this is prob-

ably an artefact of captivity and rare in nature (Liske and Davis 1987). Earlier workers suggested that copulation may be stimulated in the male if the head is eaten as this releases inhibitory stimuli and they also referred to the fact that the male's copulatory movements are controlled by the last abdominal ganglion so that mating may continue after most of the body has been eaten.

The eggs, numbering from 10 to 400 or more according to the species, are laid in an ootheca formed from a moist frothy material produced by the accessory glands and moulded by the ovipositor valves. This becomes a hard horny material on drying and is often enclosed in a soft spongy ball. Ranged along the mid-dorsal line of the ootheca is a series of apertures, covered by exit caps, leading into subvertical chambers containing the eggs. Once fertilised a female may lay a number of oothecae. The size and shape of the ootheca and its deposition site is usually species specific. It is commonly attached to a flat substrate such as a tree trunk or a fence but may be built around a twig or group of grass stems or deposited in the ground or under rocks or wood on the ground. The female usually leaves the ootheca immediately it has been laid but in a few species she remains on guard over the ootheca and even 1st instar nymphs, thus reducing the incidence of parasitism and predation.

Obligatory parthenogenesis has been recorded for an American species in which males are unknown (M. J. D. White 1951). Unfertilised females of other species frequently lay infertile oothecae under caged conditions.

Nymph. After the intermediate moult, the nymph behaves in essentially the same way as the adult, feeding upon small, soft-bodied insects. Regeneration of lost appendages may occur, particularly in early instars. The nymphal period lasts some weeks or months.

Natural Enemies. The eggs of Mantodea are often heavily parasitised by proctotrupoid and chalcidoid Hymenoptera. In Australia the latter are represented especially by species of *Podagrion*. Their small circular emergence holes may often be seen studding the surface of oothecae. Chloropid flies are often bred from oothecae, but whether they are parasites or only scavengers is not clear; in Australia, numerous *Botanobia tonnoiri* (Chloropidae) have been reared from oothecae of *Tenodera australasiae*. Crickets, ants, dermestid beetles, small mammals and birds are known to prey on the ootheca. Very young nymphs are subject to high mortality due to predation by other insects and also from weather extremes. Later stages are subject to predation by birds, lizards, insectivorous mammals, and sphecoid wasps, and to parasitism by mites and mermithid nematodes.

Defence Mechanisms. A number of defence mechanisms have been recorded for the Mantodea. These are summarised and categorised by Robinson (1969) and Edmunds (1976). Primary defensive adaptations, which reduce the probability of a predator attack, include camouflage, warning coloration and colour mimicry.

Morphological adaptations for mimicry include bark, stick, grass and leaf mimicry. Early nymphs of a number of species derive protection by mimicking ants in colour and behaviour.

Secondary defensive adaptations, used when under attack or threat of attack, include active running, jumping or flying to escape, thanatosis, chemical defence by regurgitation of fluids at the mouth, flash coloration and startle display. Startle display includes raising the front part of the body, lifting the wings to produce an apparent increase in body size and also often to display brilliant colours or eyespots, flexing of the fore legs to suddenly reveal bright colour markings, and stridulation by rubbing the sides of the abdomen against the hind wings to produce a hissing noise.

A final defensive mechanism is overt attack involving striking at the predator with the fore legs or biting with the jaws.

Economic Significance. Mantid numbers in nature are so low that they can have little economic significance. Attempts have been made to breed them commercially as biological control agents, but mantids are non-specific predators and will consume beneficial insects as well as pest species.

Polymorphism, Colour Adaptation. Little is known of the factors controlling body colour in mantids but in some species it appears to be genetic and in others environmental. Many, particularly flower dwellers, can change their colour over a number of days to match their background, and melanism as a result of fire is not

uncommon. Colour polymorphism occurs in some species, green and brown being the principal colour alternatives. These two colours would have survival value according to the season in monsoon savanna lands.

Ecological Features. The density of mantodean populations is low, possibly because of the high incidence of egg parasitism and the vulnerability of the early nymphal instars. Cannibalism is frequent in cultures, and could be expected to occur in the field as densities increase. Feeding is not concentrated upon particular prey species and in general prey is not actively sought out. In these circumstances the predator could not be expected to bear heavily upon any prey species, and its own population regulation is likely to be brought about in the main by agencies other than food shortage.

Special Features of the Australian Fauna

The mantid fauna of Australia consists of 3 families and 5 subfamilies, none of which is endemic. Australian records of the amorphoscelid subfamily Amorphoscelinae and the mantid subfamilies Thespinae, Comptosiespinae and Toxoderinae are considered doubtful (Balderson 1984). No introduced mantids have been recorded for Australia, and 21 of the 37 recognised genera are endemic. Generic and species diversity is greatest in northern Australia and declines to very few species in cooler regions.

CLASSIFICATION

Order MANTODEA (162 Australian spp.)

Chaeteessidae (0)	1. Amorphoscelidae (45)	3. Mantidae (116)
Metallyticidae (0)	Eremiaphilidae (0)	Empusidae (0)
Mantoididae (0)	2. Hymenopodidae (1)	

The classification followed here is basically that of Beier (1964) which recognises 8 families and 26 subfamilies world-wide. Studies of major importance on Australian mantid taxonomy are those of Beier (1935a,

1935b, 1964), Giglio-Tos (1913, 1927), Tindale (1923–24) and Westwood (1889). Further works by these authors together with all other relevant literature on the Australian mantid fauna are given in Balderson (1984).

Key to the Families and Subfamilies of Australian Mantodea

1. Ventroexternal margin of fore tibia without spines **Amorphoscelidae-PARAOXYPILOINAE**
- Ventroexternal margin of fore tibia with a row of spines 2
- 2(1). Ventroexternal spines of fore tibia reclinate and closely spaced **Hymenopodidae-ACROMANTINAE**
- Ventroexternal spines of fore tibia erect and widely spaced **Mantidae. 3**
- 3(2). Margins of pronotum straight, widening slightly anteriorly **ORTHODERINAE**
- Margins of pronotum not straight, usually with pronounced supra-coxal widening 4
- 4(3). Fore femur with 3 discoidal spines **IRIDOPTERYGINAE**
- Fore femur with 4 discoidal spines **MANTINAE**

1. Amorphoscelidae. The Australian species, which belong to 8 genera in the subfamily PARAOXYPILOINAE, are small mantids that mostly live on the ground or tree trunks where their cryptic coloration makes them difficult to detect. Males are fully winged and, in most species, females are apterous or brachypterous. Apterous females of *Cliomantis* (Fig. 21.6) closely resemble males but apterous females of *Paraoxyphilus* are markedly dissimilar to males (Fig. 21.7). While at rest, *Paraoxyphilus* females frequently engage in 'boxing' displays, extending and

flexing the fore legs alternately and, in some species, showing bright colour markings on the inner face of these legs. It is thought that this is probably a territorial display helping to space out individuals of the species. Females of *Nesoxypilus* from northern Australia are apterous and mimic ants (*Rhytidoponera*), running in short sharp bursts with foraging ants and displaying ant-like antennal movements. It is uncertain whether this mimicry assists the mantids to prey on ants or serves to protect the mantids from predators. Both sexes of *Gyromantis* have promi-

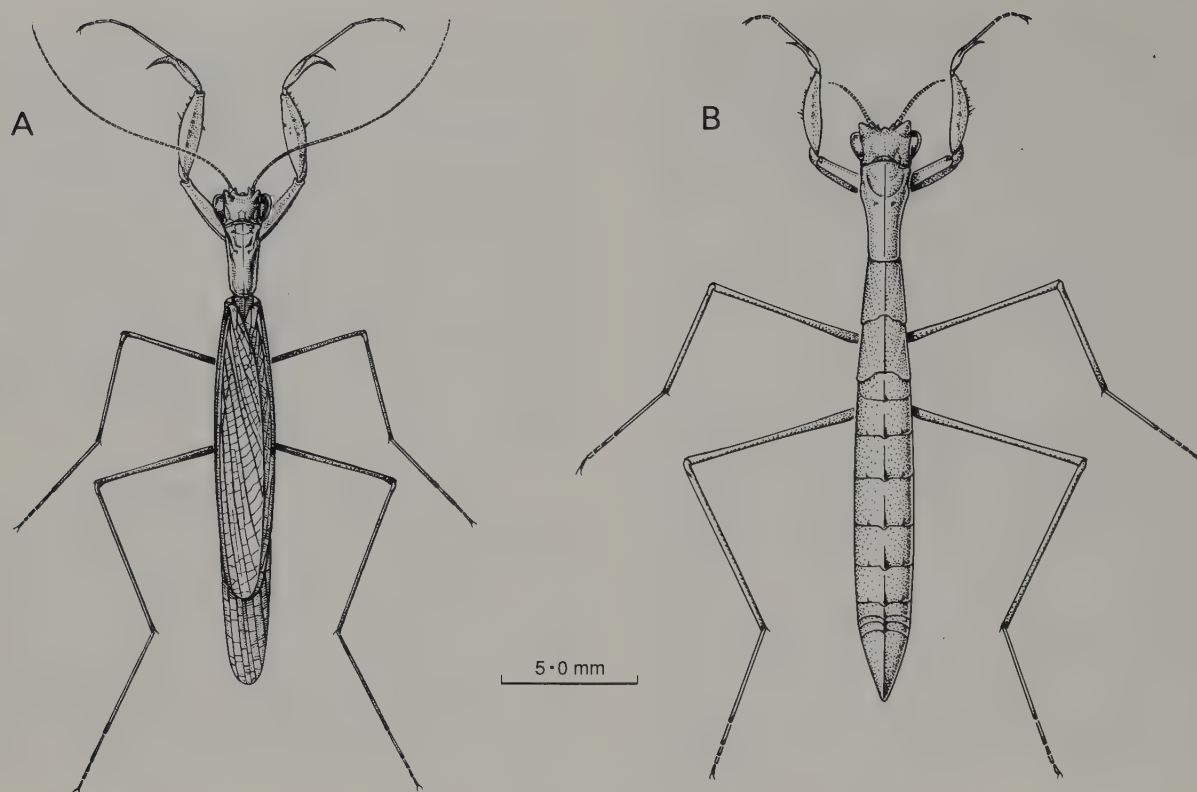


Fig. 21.6 *Cliomantis cornuta*, Amorphoscelidae, dorsal views: A, ♂; B, ♀.

[A by F. Nanninga; B by G. Milledge]

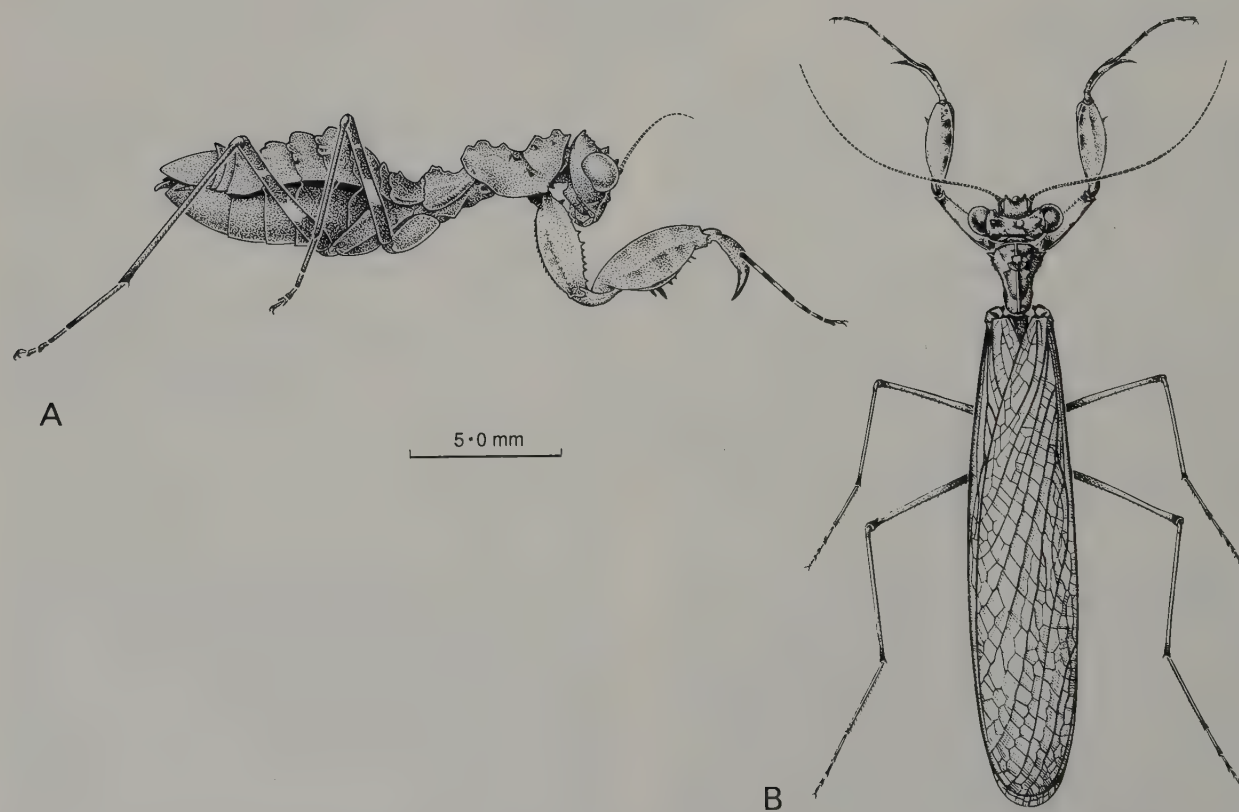
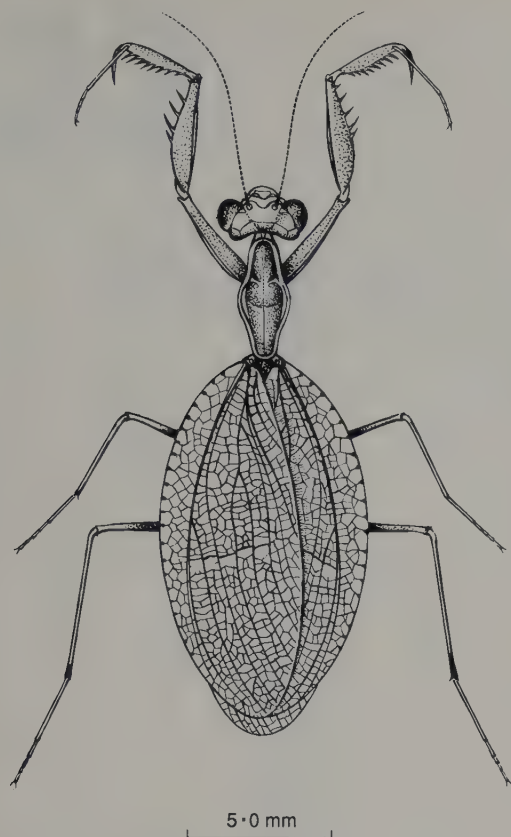


Fig. 21.7 *Paraoxyphilus tasmaniensis*, Amorphoscelidae: A, ♀, lateral view.; B, ♂, dorsal view.

[A by F. Nanninga; B by G. Milledge]

Fig. 21.8 *Neomantis australis*, Mantidae, ♂.

[F. Nanninga]

nent short spines on the head and pronotum. The oothecae in this genus are very long and narrow and are attached to tree trunks (Fig. 21.4A).

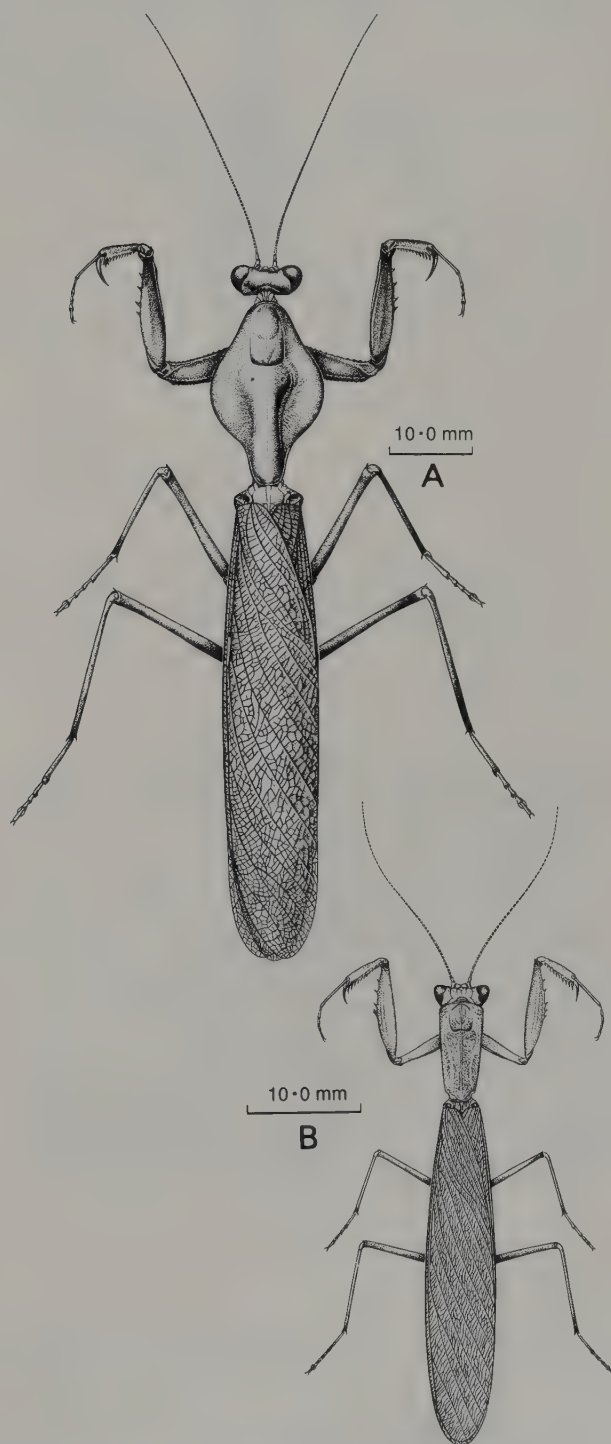
2. Hymenopodidae. *Acromantis australis* from the rainforests of North Qld is the one Australian representative of this large tropical genus of the subfamily ACROMANTINAE. It is a small mantid with a small flattened lobe on the middle and hind femur and a prominent spine projecting anteriorly from the vertex.

3. Mantidae. This family includes almost three quarters of the Australian mantid species. They range from small delicate rainforest forms to large voracious species that can catch and eat small lizards and frogs.

The ORTHODERINAE (2 genera, 7 spp.) are essentially Australian and are medium sized green mantids. The widespread and cosmopolitan *Orthodera ministralis* (Fig. 21.9A) has a bright blue to purple spot on the inner face of the fore femur. Its hard 'woody' ootheca (Fig. 21.4G) is commonly found attached to fences and walls of buildings.

The IRIDOPTERYGINAE (9 genera, 42 spp.) are mostly small fragile-looking mantids and are found mainly on shrubs or tree trunks. The widespread genus *Bolbe* consists of several very small species including *B. maia* which may measure as little as 8 mm. Females are apterous and ground dwelling. The remaining genera are mainly tropical or subtropical. *Neomantis* (Fig. 21.8)

and *Kongobatha* are dainty, pale, leaf-green, shrub-frequenting mantids. Males of *Calofulcinia* fly and run very actively; females are apterous and well camouflaged to blend into mossy substrates. *Ciulfina* comprises a number of cryptically coloured species that further conceal themselves by lying flat against tree trunks so that they cast no shadow. They are long legged and when disturbed run exceptionally quickly around the tree trunk. This

Fig. 21.9 Mantidae: A, *Orthodera ministralis*, ♀; B, *Hierodula atricoxis*, ♂.

[F. Nanninga]

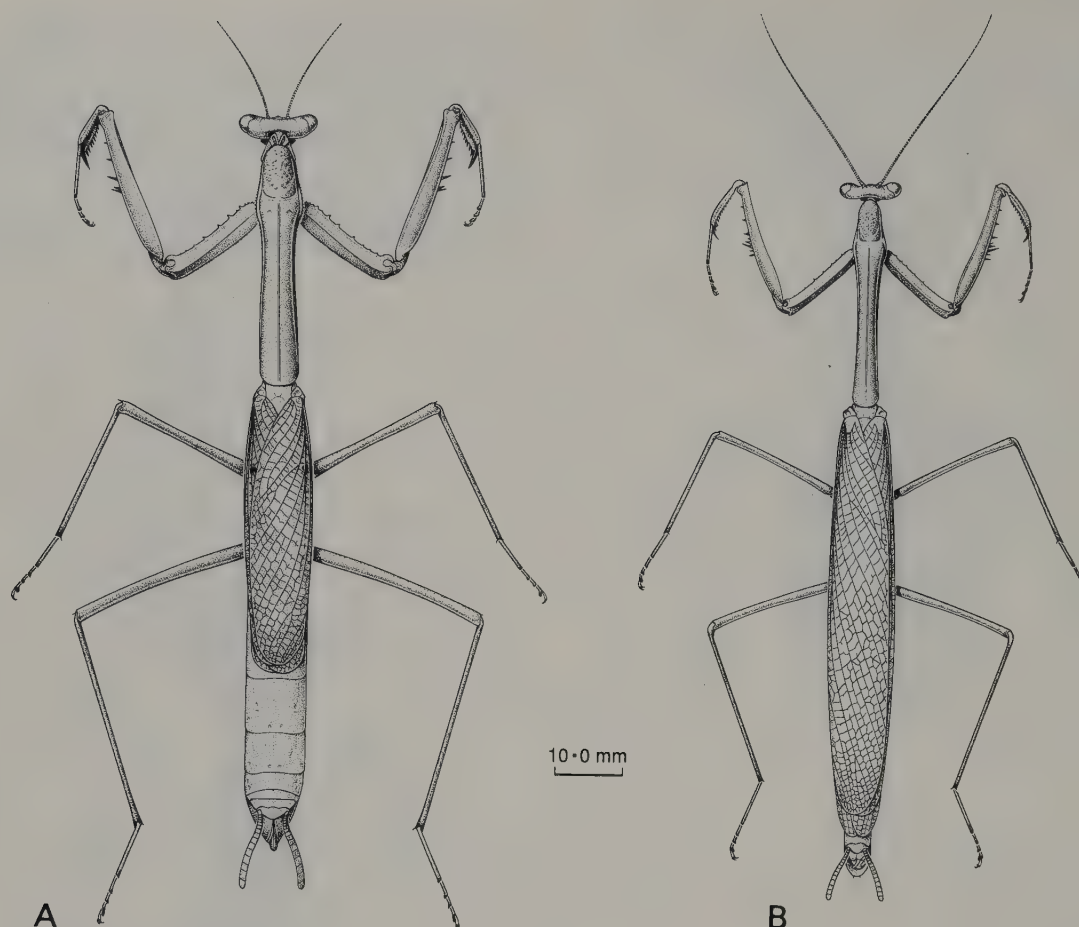


Fig. 21.10 *Archimantis latistylus*, Mantidae: A, ♀; B, ♂.

[G. Milledge]

speed is also used in actively pursuing prey. The oothecae of Iridopteryginae are small and elongate and are mainly attached to tree trunks (Fig. 21.4B).

The MANTINAE (17 genera, 67 spp.) is a large subfamily of medium to large and slender to robust species. A number of genera are endemic but others are more widespread overseas. *Mantis octospilota*, usually with eight broad black spots on the dorsal surface of the abdomen, is the sole representative of a genus widespread through Europe, Asia and Africa. *Hierodula*, a large genus of mantids in tropical Asia and Africa, has some eight species in northern Australia (Fig. 21.9B). Similarly, *Tenodera* with two Australian species, is widespread throughout Asia and has been introduced into North America. *T. australasiae* (Plate 2, A) is a large species

widely distributed in Australia and is common in suburban gardens. *Archimantis* with eight species is wholly endemic to Australia and includes two large, widespread species, *A. latistylus* (Fig. 21.10) and *A. sobrina*. Males in this genus are fully winged but females are brachypterous. Their ootheca (Fig. 21.4D) is a large spongy ball and is attached to grass stalks and twigs. Despite its name, *Nullabora flavoguttata* is widespread though not common in the arid and semi-arid interior of the continent. It has a very thin anteroposteriorly flattened head and pointed eyes. *Rhodomantis* is a genus of very slender, long-legged, stick-like mantids usually associated with spinifex and other low grasses and shrubs in drier regions. Species of this genus and of *Sphodropoda* have been recorded ovipositing in sandy soil.

Grylloblattodea

Grylloblattida, Grylloblattaria, Grylloblattoidea, Notoptera

D. C. F. RENTZ

Apterous, mandibulate, exopterygote Neoptera, having all legs cursorial, with large coxae; pronotum without descending lateral lobes; auditory organs absent; cerci long, flexible, segmented; S9 of male bearing articulated coxites; ovipositor strongly projecting. Eggs free; nymphs subterranean.

The Grylloblattodea or ice crawlers are a small group of soft-bodied, apterous, terrestrial insects found under rocks and in litter in forests in cooler parts of the Northern Hemisphere. In the northern U.S.A., southern Canada, China, Siberia and Japan they occur in soil in montane habitats under low temperatures. In Korea and Japan, species have been also found in caves. Grylloblattids are slender, slightly depressed and finely pubescent; adults range in size from 2–3.5 cm in length (Fig. 22.1). They are active and carnivorous. They combine primitive characters of cockroaches and orthopterans in addition to having a highly specialised life-style (Zeuner 1939). Grylloblattids were linked first to the orthopteroid groups, but a relationship to Dermaptera was indicated by Giles (1963). The intricate anatomical study of Nagashima (1982) suggests an orthopteroid relationship but, surprisingly, it concludes that Grylloblattodea are not a primitive group. The embryological work of Ando and Nagashima (1982) and the anatomical investigation of the spermatozoa by Baccetti (1982, 1987b) demonstrate that grylloblattids are similar in these respects to some orthopteroid insects and quite different from the Dermaptera. Storozhenko (1989) compared modern grylloblattids with the Mesozoic *Blattogryllus karatavicus*; on the basis of a number of structures he concluded that the two groups were related, and represented offshoots of the Protoblattodea-Protoperlaria-Paraplecoptera complex, which extends back to the Carboniferous. Ando (1982) contains

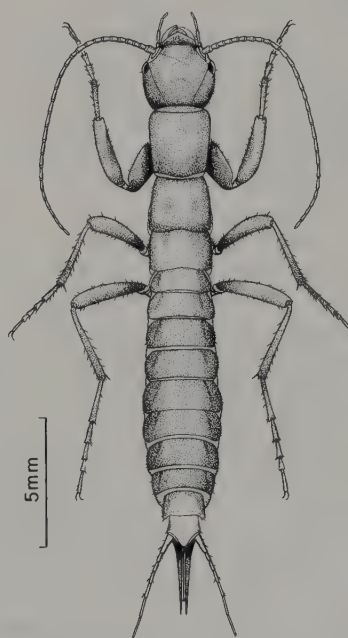


Fig. 22.1 *Grylloblatta campodeiformis*, ♀, U.S.A.

[F. Nanninga]

comprehensive accounts of the systematics, morphology and biology of the order and a complete bibliography. Storozhenko (1986) provided a catalogue of species, and

(1989) presented additional references and keys to all extant taxa.

Anatomy of Adult

The anatomy of *Grylloblatta* was studied in detail by E. M. Walker (1931–56) and of *Galloisiana* by Nagashima (1982). McIver and Sutcliffe (1982) described the sensillae of *Grylloblatta campodeiformis*.

Head. Flattened, prognathous. The resemblance of the head capsule of grylloblattids to that of Dermaptera has been shown to be merely based on the fact that they both carry a prognathous head. The head capsule is typical of orthopteroid orders. Antennae filiform, consisting of 28–39 segments; scape emanating from near base of mandible. Slifer (1976) studied the sensillae on the antenna of *Grylloblatta*. Mandibles large, heavily sclerotised, apically pointed, lacking molar region commonly found in orthopteroid insects; maxilla large, projecting slightly beyond tips of mandible; galea bears 10 small hairs along outer margin; lacinia curved similarly to galea, well sclerotised, deeply pigmented with one or two small teeth subapically; maxillary palp 5-segmented; labium composed of 3 plates, prementum, mentum and postmentum; paraglossa and glossa separated from prementum by a fine suture. Ocelli absent. The eye of *Galloisiana* has been studied in detail by Gokan *et al.* (1982). The number of ommatidia constituting an eye varies individually and is less in young instars. Adults of *Grylloblatta* typically have 70 ommatidia; those of *Galloisiana* have 40. Some cave-dwelling species lack eyes.

Thorax. The 3 segments are similar, free, the prothorax the largest. Terga flattened, pronotum without descending lateral lobes. Sternum with several separate sclerites joined by membrane. Pleura oblique; in the prothorax small, in meso- and metathorax weakly sclerotised. Meso- and metathoracic spiracles present.

Legs. All pairs similar, cursorial. Coxae large, ventrally separated. Tarsi 5-segmented, considered a primitive character, with ventral membranous pads and terminal claws lacking an arolium.

Abdomen. Consisting of 11 segments; first free from the metathorax and bearing an eversible sac. T10 is the supra-anal plate; T11 is the depressed and vestigial epiproct; paraprocts poorly developed. Cerci long, flexible, 5–9-segmented in adults, this being considered a primitive character in orthopteroid insects. Spiracles present in the pleural membrane of segments 1–8. In males, S9 constitutes the subgenital plate and bears a broad, triangular, scoop-shaped left coxite and a narrower, more digitiform right one, each with a terminal style. The asymmetrical genitalia, freely exposed between the coxites, comprise principally a right lobe (right phallomere) bearing irregular, sclerotised processes and a left lobe (left phallomere) with an eversible, membranous sac; left coxite larger than right coxite. In females, S8 is not extended backwards to form a subgenital plate; the projecting rigid ovipositor consists of 3 pairs of slender, tapering, partly free valves.

Internal Anatomy. Head with 47 pairs of muscles; head musculature not showing particularly primitive fea-

tures except in that of mandible. Central nervous system consists of 3 thoracic and 7 discrete abdominal ganglia. Salivary glands apposed to oesophagus and without a reservoir. Alimentary canal with large crop and muscular gizzard; mid gut short and broad with 2 ill-defined caeca anteriorly. Malpighian tubules 12–24 in *Grylloblatta campodeiformis*, opening independently into the intestine.

Karyotype. For *Galloisiana nipponensis*, 30 diploid chromosomes with XY sex mechanism (Nakamura 1946).

Immature Stages

The eggs of grylloblattids are large, black and laid singly. They develop over periods ranging from 5 months to 3 years. There is a large quantity of cytoplasmic reticulum and periplasm, which is typical of orthopteran eggs. The pattern of embryogenesis resembles that of some orthopterans (Ando and Nagashima 1982) and differs from that of dermapterans. Baccetti (1982) found that the spermatozoa of grylloblattids resembled that of orthopterans more than cockroaches or dermapterans. All nymphal instars lack euplantulae (pulvilli) on tarsal segments. There are eight nymphal instars and development takes up to 7 years. The number of antennal segments, hind femoral length, number of cercal segments and the setal composition of the cercus change with the instar and the stage of development can be discriminated readily (Yamasaki 1982a). In sighted forms, the number of ommatidia also changes with the instar. Young instars are white, subadults creamish white, adults brown or black depending on the species.

Biology

Grylloblattids are cryptozoic, preferring wet habitats under low temperatures. They were said to be fundamentally nocturnal but are apparently active both day and night. *Grylloblatta* lives beneath stones, on the fringes of snow banks, in rock crevices of montane talus slopes, in ice caves and volcanic lava tubes and in rotting logs (Rentz 1982). They are almost all found at high altitudes. During winter adults and nymphs probably occupy the airspace between the ground surface and overlying snowpack, and they may well remain active at the 0°C constant temperature prevailing there (J. S. Edwards 1982). They enter winter with massive fat body deposits but they may encounter food in the form of frozen insect bodies which are present in rock fissures. In spring, with the melting snowpack, *Grylloblatta* becomes a nocturnal forager feeding often on the frozen bodies of windblown insects on the snow surface. They also eat amounts of plant material (Pritchard and Scholefield 1978).

Although grylloblattids prefer cool temperatures, their capacity to withstand subzero temperatures is limited. The supercooling point of grylloblattids collected on Mt Rainier, Washington, U.S.A. in summer is -5.5 to -8.5°C. They do not have significant levels of glycerol, sorbitol or erythritol in the haemolymph and are killed by the formation of ice within the body (Morrissey and Edwards 1979). In winter they are covered by a deep insulative layer of snow and probably do not experience temperatures much below 0°C.

Korean grylloblattids have all been recorded from caves although these may well be terrestrial forms (Namkung 1982). Some have been taken in caves under 200 m altitude with mean air temperatures ranging from 10–15°C. The Korean species occur under stones and debris on the floor of the caves.

In Japan *Galloisiana nipponensis* is the most common grylloblattid and its life history has been studied in detail (Nagashima *et al.* 1982; Yamasaki 1982b). It occurs at 300–3000 m elevations in central Japan and occurs under stones and wood in the shade of thick, mixed hardwood and coniferous forests, in subalpine zones, and in caves. There is no winter dormancy. The mean minima and maxima atmospheric temperatures in these habitats range from 9° to 19°C. *Galloisiana* prefers regions at and below 12°C in yearly mean air temperature. Soil temperatures at depths of 10 cm range from 7.5° to 8°C. Last nymphal instars appear from July to September with adults appearing from September to November. Males appear about a month later than females. They appear to be active day and night and show no nocturnal preference. They are carnivorous, consuming a variety of insects dead and alive and some plant material.

Copulation. Nagashima *et al.* (1982) provides a detailed description and colour photographs of the copulation of *G. nipponensis*. Briefly, the sequence of events is as follows: after a chase, the female is seized by the male. Copulation lasts from 30 minutes to 4 hours. Males always take their position on the right side of the female

during copulation. This is probably due to the asymmetry of the male external genitalia in the 9th abdominal segment. The eversible sac of the male left phallomere is inflated during copulation.

Oviposition. Oviposition occurs 10–50 days after copulation. Females lay eggs in wood or under stones and decaying leaves. None have been found in moss. Oviposition of each egg takes about 3 minutes. Females lay 5–6 eggs a day and a total of about 30 in an ovipositional series. A captive female laid a total of 145 eggs.

CLASSIFICATION

Since the 1st edition of this book, the grylloblattids have been represented in the literature under five ordinal names. There is one extant family, Grylloblattidae, containing four genera: *Grylloblatta** with 11 species from the montane regions of western North America; *Grylloblattina* with one species from Siberia; *Galloisiana* with 10 species from Japan, Korea and Siberia; and *Grylloblattella* with three species from the Siberia, China and Korea. The group is undoubtedly more widespread, and nymphs from many other localities probably represent several undescribed species. No grylloblattids have been discovered in the Southern Hemisphere.

* Vickery and Kevan (1983) placed *Grylloblatta* in its own subfamily, the Grylloblattinae.

Dermaptera*

(*Earwigs*)

D. C. F. RENTZ and D. K. McE. KEVAN

Elongate, prognathous, winged or apterous, exopterygote Neoptera, with cerci modified into terminal forceps; thorax with many free sclerites; when present, fore wings reduced to small tegmina, and hind wings membranous, semicircular, almost entirely made up of anal fan, and almost completely folded beneath tegmina at rest; legs relatively short, cursorial, tarsi 3-segmented; abdomen long, freely movable, telescopic.

Some 1800 species of Dermaptera have been described from all parts of the world (except the polar regions), but only about 60 are known from Australia. All are elongate and flattened, the mobile, telescopic abdomen ending in a pair of forceps (Fig. 23.1). They range from approximately 7 to 50 mm long, and vary in colour from buff to black. They favour damp, confined spaces and are largely nocturnal. Their relationships have been investigated by Giles (1963), who concluded that they are closer to the primitive Grylloblattodea than to any other orthopteroid order. This is supported by a number of subsequent authors including Matsuda (1976) (see Vickery and Kevan 1983, 1986), but not necessarily by recent investigations on the anatomy and embryology of the Grylloblattodea (Ando 1982; see also Chapter 22), or the micromorphology of the spermatozoa (Baccetti 1987b).

Anatomy of Adult

Head. Broad, flattened, freely movable on neck; prognathous, with typical mandibulate mouth-parts. Compound eyes large in Forficulina, small or wanting in other suborders; ocelli wanting. Genae much reduced in front of eyes, but much inflated behind; Y-shaped ecdysial line usually conspicuous on vertex. Antennae of

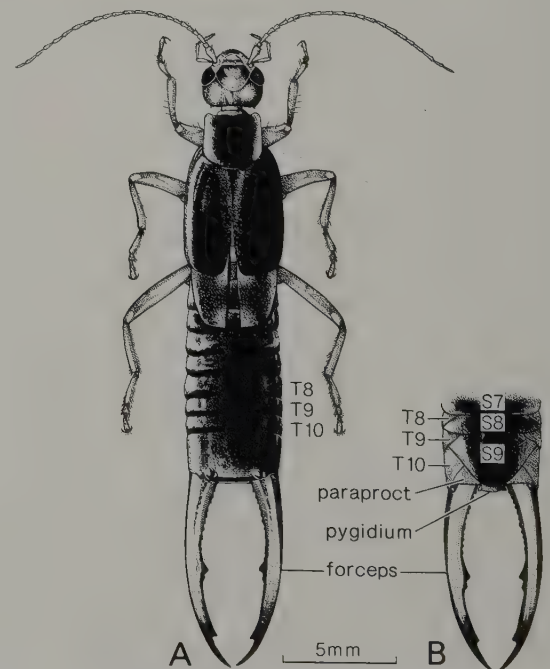


Fig. 23.1 *Labidura truncata*, Labiduridae, ♂: A, dorsal; B, terminal segments, ventral.
[T. Nolan]

* Some parts of this chapter are adapted from Giles (1970, 1974a) and Webb (1974).

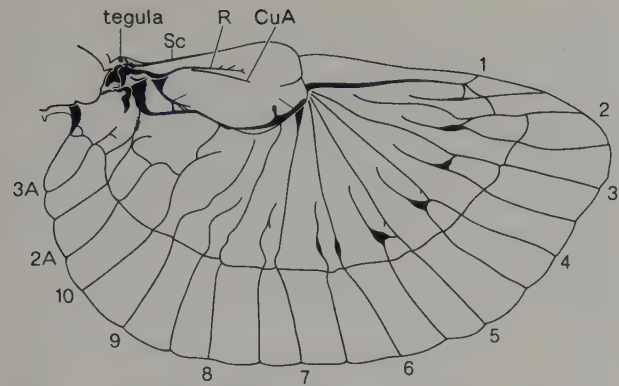


Fig. 23.2 Hind wing of *Echinotoma* sp., Pygidicranidae. [After Giles 1963]

short annulate type. Clypeus divided into sclerotised postclypeus and membranous anteclypeus. Mandibles with 2 apical teeth; inner edge with distal incisor region and proximal molar area, except in *Arixeniina* and *Hemimerina*. Parts of maxillae much divided and primitive. Hypopharynx with 3 distal lobes. Labium large, primitive, without glossae, but with gula attached and almost covering ventral surface of head. Neck cylindrical, unprotected, with 3 series of sclerites.

Thorax. Segments free; pro- and mesothorax subequal, metathorax largest; generally primitive, with many free sclerites. Fully winged species with large pronotum having ecdysial line; mesonotum small, comprised mainly of scutum; metanotum large, also comprised mainly of scutum, with 2 lines of bristles to lock tegmina at rest. Apterous species with large pronotum, small mesonotum, and still smaller metanotum, all having ecdysial line. Pleura always exposed, with many free sclerites and fairly extensive membrane; 2 pairs of spiracles in membrane. Sterna increasing in size from front to rear, metasternum very large, overlapping from front to rear; intersegmental sclerites small.

Legs. Fairly short, subequal. Coxae widely separated and short. Tarsi 3-segmented, 1st and 3rd tarsomeres long and 2nd very short. Euplantulae, pulvilli, arolium and empodium usually lacking. Pretarsal claws long.

Wings. Tegmina, when present, small, smooth, lacking definite veins. Hind wings, when present, large, almost entirely membranous, semicircular (Fig. 23.2), at rest folded fanwise and then longitudinally beneath tegmina, except for sclerotised squamae. Pre-anal veins of hind wing very much reduced and confined to partly sclerotised remigium. Flying membrane consisting of the very large anal fan supported by 10 radiating branches of 1A; 2A and 3A short, simple; intercalaries present between branches of 1A and between 2A and 3A; cross-veins linking each element of anal veins.

Abdomen. Long, freely movable, telescopic, depressed, with 10 segments visible dorsally in male, but only 8 in female, in which terga and S8 and S9 are reduced and fused to T10; forceps usually more curved and often larger or heavier in male (Fig. 23.1) than in female (Fig. 23.3). Terga overlapping for about one-third of their lengths; T10 strongly sclerotised, rectangular.

Sterna similarly overlapping; S1 wanting. Subgenital (or subanal) plate represented by S9 in male and by S7 in female; large, triangular in both sexes (Figs 23.1, 3); in male sclerotised, wire-like loop developed in middle of anterior margin for attachment of genitalic muscles. Pleural sclerites absent; tergum overlapping sternum laterally in each segment; 8 pairs of spiracles present in membrane. Triangular paraprocts present at base of forceps, which are separated by epiproct consisting of 2 plates: anterior dorsal pygidium and posterior ventral metapygidium.

GENITALIA. In male (Fig. 23.4), lying in genital chamber above subgenital plate (S9), and consisting of large, subcylindrical, partly sclerotised organ, with basal section single and concealed within body wall and distal section, or penis, forked apically. In primitive labidurids (Fig. 23.4A) each penis further divided into a sclerotised medial lobe traversed by a *virga* (sclerotised terminal portion of the ejaculatory duct) and heavily sclerotised lateral lobe;

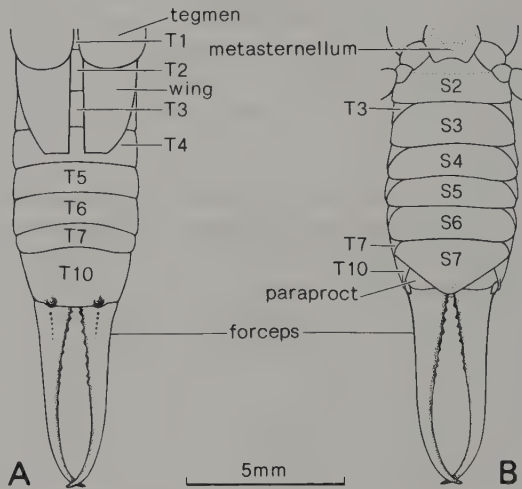


Fig. 23.3 Abdomen of *Labidura truncata*, ♀: A, dorsal; B, ventral. [T. Nolan]

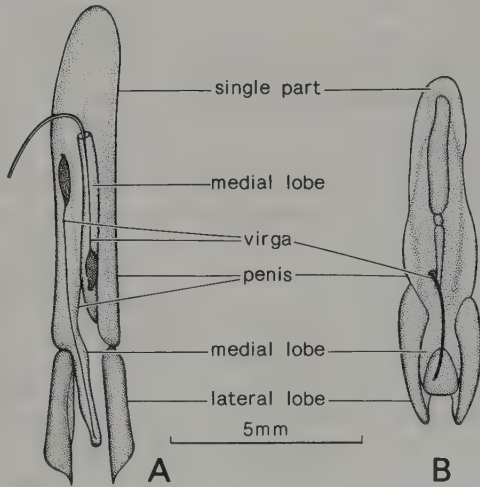


Fig. 23.4 Male genitalia, diagrammatic, of: A, *Labidura truncata*; B, *Forficula auricularia*, Forficulidae. [B. Rankin]

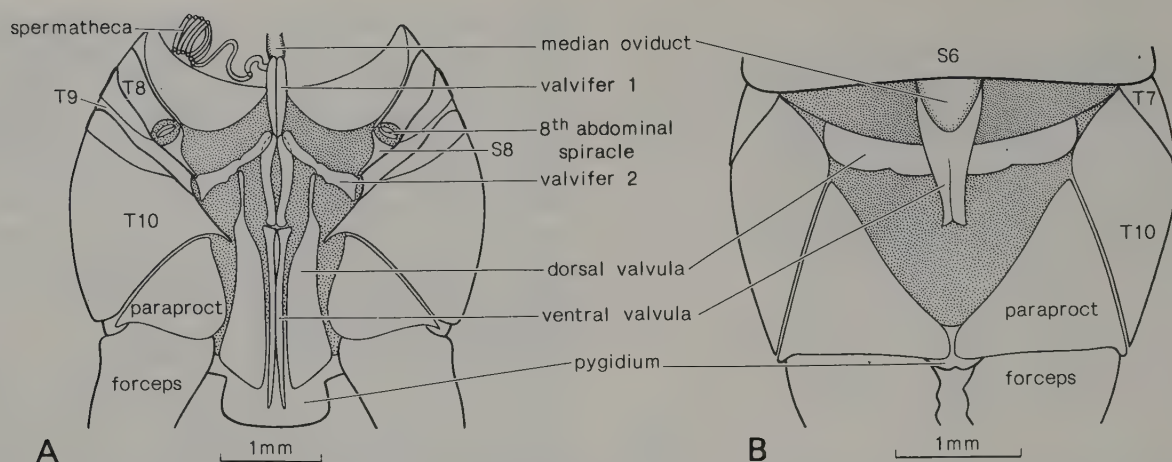


Fig. 23.5 Female genitalia, diagrammatic ventral view with subgenital plate (S7) removed, of: A, *Echinotoma* sp. (after Giles 1963); B, *Labidura truncata*.

[B. Rankin]

in more specialised forficulids (Fig. 23.4B), Arixeniina and Hemimerina, with one medial lobe lost and associated virga aborted to varying degrees. Number and ornamentation of medial lobes, shape of lateral lobes, and structural details of virga all of taxonomic importance. In female (Fig. 23.5), ovipositor always much reduced and concealed by subgenital plate, except in most Pygidicranidae in which valves project slightly; comprised of 2 pairs of valves, flattened laterals and rod-like medials (probably representing dorsal and ventral valvulae respectively). In both sexes the genitalia are unique among orthopteroids.

Internal Anatomy. Alimentary canal typical of orthopteroid insects; showing all usual regions, except for reduced salivary glands and lack of gastric caeca. Antennal circulatory system (in at least 3 unrelated species) of a functional type unique in insects (Pass 1988); an independent organ exists for each antenna consisting of a pulsatile ampulla connected to an antennal blood vessel; the involvement of a precerebral fronto-pharyngeal muscle suggests an ancestral condition. Central nervous system with brain, suboesophageal ganglion, 3 thoracic and 6 abdominal ganglia, all joined by thick connectives. Tracheal system without air sacs. Malpighian tubules long, slender, numerous in haemocoel, opening into commencement of hind gut in 4 groups; fat body diffuse and large, particularly prior to breeding season. Female reproductive organs simple, comprised of paired ovaries and lateral oviducts, median oviduct, spermatheca and genital chamber; single genital aperture between abdominal segments 7 and 8. Ovarioles polytrophic with two types of arrangement in the ovaries: either (as in *Forficula auricularia*) with numerous, short ovarioles in 3 series around oviduct, or (as in *Labidura truncata*) with a few, long ovarioles branching together in a linear series from end of lateral oviduct. Suborder Forficulina oviparous, but Arixeniina and Hemimerina exhibiting pseudoplacental viviparity. Male reproductive organs complex; some portions paired, but extent variable even within families; composed of paired testes, paired vasa deferentia, paired or single vesicula seminalis, and paired

or single common ejaculatory duct ending in sclerotised virga.

The micromorphology of the spermatozoa is considered by Baccetti (1987b).

The anatomy of certain Dermaptera has been studied by Giles (e.g. 1963, 1965). Most of his figures apply equally well here, for the order is notably uniform. Chopard (1949c), Beier (1959), Günther and Herter (1974), W. L. Brown (1982), Vickery and Kevan (1983, 1986) and Steinmann (1986) have given good general accounts of the order.

Polymorphism. Many species of earwigs are polymorphic in wing development (Kleinow 1966, 1971) and (especially in males) the relative length of the cerci (forceps) (Bateson and Brindley 1893; Sopp 1905; Diakonov 1925; Kuhl 1925, 1928; Huxley 1927; Heerdt 1953; Ollason 1972; Lamb 1976; Terata and Sakai 1988).

Karyotype. The chromosomes of Australian Dermaptera were discussed by Webb (1974). In general, earwig chromosomes are small and probably holocentric. This is in contrast to other blattoid-orthopteroid orders which have large, monocentric chromosomes. The suborders Hemimerina and Arixeniina, have, respectively, the lowest and highest chromosome counts yet found in the Dermaptera; the karyotype of *Hemimerus bouvieri* is $2n\delta = 7(2AA + X_1X_2Y)$; that of *Arixenia esau* is $2n\delta = 60(29AA + XY)$ (M. J. D. White 1971, 1972). There is a wide range in between (Sakai 1987; Sakai *et al.* 1988).

Karyotypes of Australian Dermaptera can be useful taxonomic characters. The species known as *Nala lividipes*, in Australia, may prove not to be conspecific with representatives given the same name in other parts of the world, for the karyotypes vary from that given for Australia $2n\delta = 34(A^L A^L + 15AA + XY)^*$, to $2n\delta = 37(17AA + X_1X_2Y)$ for Spain and $2n\delta = 40(A^L A^L + 18AA + XY)$ for India. *Labidura riparia*, s.l., likewise, may not be a single species, for karyotypes with $2n\delta = 12(5AA + XY)$ are known from Spain and $2n\delta =$

* A^L represents a larger autosome.

14(6AA + XY) from India and Japan. The now separated *L. truncata*, with $2n\delta = 10(4AA + XY)$, has the lowest number of chromosomes (all comparatively large) yet found in the Forficulina (Giles and Webb 1972). The cosmopolitan *Euborellia annulipes* has $2n\delta = 24(11AA + XY)$. An unidentified species of rainforest anisolabidid has the highest count of very small chromosomes with $2n\delta = 42(19AA + X_1X_2X_3Y)$. *Chaetospania brunneri* $2n\delta = 34(13AA + X_1X_2X_3X_4Y)$ has the greatest number of X-chromosomes yet found in the Dermaptera. Although *Dacnodes shortridgei* (Pygidicranidae) has a relatively simple karyotype with XO males $2n\delta = 11(5AA + XO)$, another, as yet unidentified, member of the same primitive family has a karyotype $2n\delta = 20(9AA + XY)$. *Nesogaster halli*, one of the relatively advanced Spongiphoridae (= Labiidae *auctt.*), also has XO males $2n\delta = 19(9AA + XO)$. Its congener, *N. ruficeps*, has $2n\delta = 21(9AA + X_1X_2Y)$. *Notolabis occidentalis* has a relatively simple complement with $2n\delta = 24(11AA + XY)$. *Parisolabis spryi* has a higher number of more complex chromosomes with $2n\delta = 32(14AA + X_1C_2X_3Y)$.

Immature Stages

Egg. Ovoid, with thin, semitransparent, smooth, creamy white chorion; up to 2 mm long in larger species.

Nymph. Apart from size, nymphs generally resemble adults. In winged species, wing pads (always small) appear in 2nd or 3rd instar. Always distinguishable from adults by lighter colour, shorter antennae, conspicuous ecdysial line on head and thoracic terga, and male-type 10-segmented abdomen with straighter female-type forceps. Sexes cannot be distinguished externally. In *Diplatys* and *Bormansia* all nymphs have long, multiarticulate cerci in place of forceps.

Biology

Earwigs occur primarily in tropical and warm temperate zones, although many are found in cooler regions. They frequent crevices under the bark of dead trees and in fallen logs, crawl beneath all kinds of debris on the ground, and may be found in the crowns of palms. They are thigmotactic, usually nocturnal, and attracted to lights at night (Brindle 1971). A few species, such as the diurnal *Chelisoches morio* and the small Spongiphoridae, are known to fly readily, but flight in earwigs is not often noted, probably due to their nocturnal habits and the short duration of flights. The forceps are used for the capture of prey, for offence and defence, and occasionally for assisting in folding the hind wings beneath the tegmina (Kleinow 1966). Food consists of a wide variety of living and dead plant and animal matter; most are probably omnivorous, but certain species appear to be carnivorous and both herbivory and saprophagy have been recorded. Overgaard Nielsen (1987) found that the European woodland earwig, *Chelidurella acanthopygia* browsed upon bark, branches and stems, 70% of its food being of vegetable and 30% of animal origin. Chopard (1938) provided a comprehensive account of earwig biology, and Brindle (1972) brought together much information on the life histories of various species.

Reproduction and Life History. A short courtship display by the male precedes copulation, which takes place with the pair facing in opposite directions with the ends of their abdomens in contact. Depending upon the species, they may also grip each other with their forceps and either move about or remain still. Spermatozoa are retained in a quiescent but viable condition in the female spermatheca from the time of copulation until the eggs are fertilised, which may be many months later. This is undoubtedly correlated with winter population trends (see below). The mechanism and control of oviposition have been studied by Caussanel *et al.* (1986).

Eggs are laid in a batch, most commonly at the bottom of a short burrow excavated by the female beneath debris on the ground. Rarely, egg batches are found in the axils of leaves or beneath the bark of trees. As earwigs are positively thigmotactic, contact stimulus is the determining factor in the choice of site, although humidity may also be involved. Egg batches are large, the number varying considerably among species (e.g. 15–27 for *Marava arachidis*, 21–80 for *Forficula auricularia*, and 60–70 for *Anisolabis littorea*). Incubation takes place in two to three weeks depending upon the climate. There is no operculum, and the chorion splits lengthwise to allow the nymph to emerge. In *Marava arachidis* the female assists the nymph to escape from the eggshell immediately after oviposition (Herter 1943).

Female earwigs exhibit maternal care, remaining in the burrow with the eggs and young nymphs, but after one or two moults nymphs must fend for themselves and the female becomes notably cannibalistic. The initial excavation of the burrow arouses a defence mechanism in the female; she will attack any moving object which approaches the nest, and the male may also be ejected. This reaction against intruders continues while the female remains in the burrow. The laying of the first egg brings into operation two further essential responses: (1) licking the eggs, and (2) collecting the eggs together should they be scattered. The licking behaviour removes fungal spores or other extraneous material from the eggshells, and eggs soon become mouldy if removed from the female.

Depending upon the species, a nymph moults either four or five times before reaching the adult stage. The period of immaturity (from hatching to the last ecdysis) varies considerably, being about 100 days in *Labidura riparia*, 40–44 in *Marava arachidis*, and 165 in *Anisolabis littorea*. In *Forficula auricularia*, the period varies from 42–49 days at 25°C to 80–90 days at 15°C.

Population Trends. For the common European earwig, *Forficula auricularia*, there is good evidence that there are fewer males than females in the population during the winter, and the same trend has been noted in *Anisolabis littorea*, a New Zealand littoral species. It is not known whether similar seasonal variation is also a feature of the population dynamics of tropical Dermaptera. For insects which copulate months before oviposition, it is of obvious selective advantage if males are fewer when living conditions become most severe.

Natural Enemies. Birds are well-known predators of

earwigs, and European naturalists have recorded bats taking them. Parasites include tachinid flies (e.g. *Triarthria*), *Mermis* (Nematoda) and *Hymenolepis* (Cestoda), but the level of natural parasitisation is not high (probably below 10%). The harmless sporozoan *Gregarina ovata* infests up to 50% of some populations of *Forficula auricularia*.

Economic Significance. It is doubtful if many of the endemic Australian species are of significant economic importance as pests. *Nala lividipes*, auctt. however, has been recorded as causing damage to field crops in Qld (Hargreaves 1970). *Forficula auricularia*, the European earwig, which is nowadays virtually cosmopolitan in cooler regions, can be a serious nuisance if present in large numbers. This earwig is sometimes regarded as being a serious pest of gardens and vegetable crops. With the advance of suburbia, and the increasingly large tracts of land coming under cultivation and irrigation, *F. auricularia* is becoming a much more serious pest than previously indicated. It eats holes in a wide variety of leafy vegetables and finds their stems and buds suitable hiding places. It feeds on fruit, often enlarging the wounds caused by wind damage or by other pests. It feeds on flower buds, often favouring *Dahlia* and roses. The European earwig often invades houses where it may sometimes chew holes in clothing and carpets. On the other hand, *Labidura truncata* has been observed in the

A.C.T. readily attacking codling moth (*Cydia pomonella*) larvae searching for cocooning sites.

Special Features of the Australian Fauna

The more primitive Pygidicranoidea are widely distributed in Australia, but the more advanced Forficuloidea are more restricted. The number of Australian species that have been described is not as large as might be expected, almost certainly as a result of inadequate collecting rather than of a poor fauna. Most have been found in the wetter regions, but *Labidura truncata* and *Nala lividipes* have been collected throughout the continent. It is apparent that there is a considerable Indo-Malayan element, particularly in northern tropical regions. There is also a fair degree of correspondence between the faunas of North Qld on the one hand and of New Guinea, the Bismarck Archipelago and the Solomon Islands on the other. Most Australian species, nevertheless, are endemic. There are noticeable differences between the known faunas of the east and the west of the continent, undoubtedly another consequence of spasmodic collecting. Except for a few short papers by Burr, Mjöberg, Hebard and Hincks, referred to in Hincks (1954), and Giles (1965, 1970) and Brindle (1987b) little has been written about Australian Dermaptera.

CLASSIFICATION

Order DERMAPTERA

(63 Australian spp.)

Suborder HEMIMERINA (0)

Hemimeridae (0)

Suborder ARIXENIINA (0)

Arixeniidae (0)

Suborder FORFICULINA (63)

PYGIDICRANOIDEA (7)

1. Pygidicranidae (7)
- Diplatyidae (0)

ANISOLABIDOIDEA (26)

2. Anisolabididae (11)
3. Labiduridae (15)

APACHYOIDEA (3)

4. Apachyidae (3)

FORFICULOIDEA (27)

5. Spongiphoridae (15)
6. Chelisochidae (8)
7. Forficulidae (4)

The Dermaptera are usually subdivided into four suborders: Archidermaptera, comprised entirely of fossils from the Upper Jurassic; Arixeniina; Hemimerina; and Forficulina, which are the typical, free-living earwigs and the only ones occurring in Australia. The Arixeniina (Fig. 23.6A) include only five species (two genera), which are associated with molossid bats in Malaysia, Indonesia and the Philippines (Nakata and Maa 1974). They either live on the bats, or frequent their roosts, but are not necessarily ectoparasitic. Species of both genera are robust, hairy, apterous, viviparous and almost blind. The forceps are rod-like, except in the males of one species. As close relatives of one of the bats involved occur in New Guinea and near Cape York, Qld, it seems possible that Arixeniina may be found in these localities in the future. The Hemimerina (Fig. 23.6B), excluded from the Dermaptera by various authors, comprise about 10 species, all of which are semi-parasitic under the fur of various species of *Cricetomys*, the giant rats of tropical Africa, and of *Beamys*, the East African mouse. Apparently there is

considerable host-parasite specificity. These insects are streamlined, depressed and smooth for rapid movement through the fur, and the tarsal segments have specially large pads for gripping the hairs. They are blind and apterous, and the forceps are cylindrical and rod-like.

Many attempts over a long period of time have been made to develop a classification of Dermaptera. A number of recent works utilising phenetic and cladistic methods have led to much controversy over the assignment of certain families and subfamilies to higher taxa. A considerable amount of splitting has occurred, and there may have been a failure to recognise homoplasy in some classifications. Burr (1911) presented a major revision of the order, and later (Burr 1915, 1916) expanded the work of Verhoeff and Zacher on the value of male genitalia in classification. Unfortunately, all species known at the time were not included. A numerical approach was taken by Blackith and Blackith (1968) and by Kamp (1973).

Popham (1965a, 1968) and Popham and Brindle (1966–69) rearranged the higher classification substan-

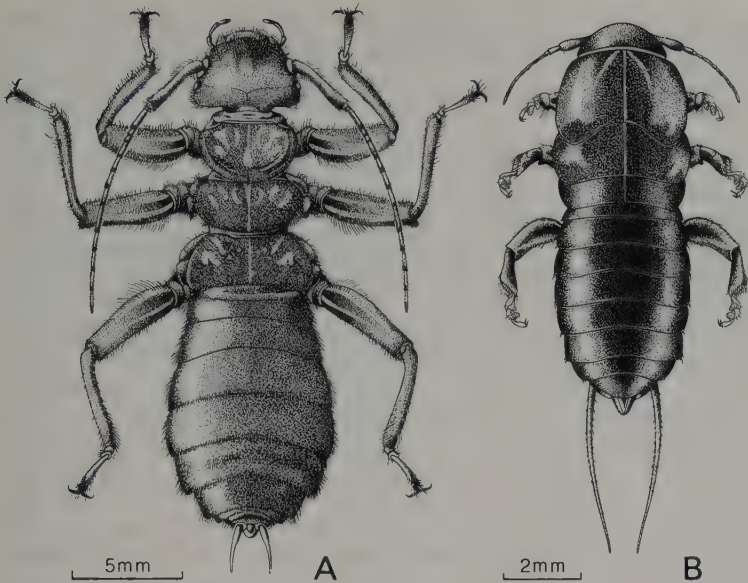


Fig. 23.6 A, *Arixenia esau*, Arixeniina, ♀; B, *Hemimerus vosseleri*, Hemimerina, ♀. [T. Nolan]

tially. Popham (1973) reiterated his view (tacitly shared by Steinmann 1986) that the Hemimerina should be treated as a separate order. Later Popham (1985) conceded that Giles (1974b) was correct in assessing the affinities of the Hemimerina, Forficulina and Arixeniina, though he still left the ordinal status of the Hemimerina open and did not recognise the last group above the family level. The cytological study of White (1971) supports Giles's view. Popham (1985) presented a cladistic classification of the Dermaptera which seems logical but differs somewhat from any other presented thus far. He repeated his previous contention (Popham 1965b) and provided evidence indicating that the arixeniid parasites should not be accorded subordinal status, maintaining that they are related to the labiids (i.e. spongiphorids) and should be included in the Labioidea (Spongiphoroidea). Unfortunately, Popham did not deal with all the subfamilies and it is difficult to know where to place some of them. About the same time as Popham, Sakai (1984) presented a different cladistic classification, but this was not formally published until later (Sakai 1987, 1988a, b). Among other differences, Sakai excluded the Arixeniidae from the Forficulina. The classification used here follows that of Günther and Herter (1974), Vickery and Kevan (1983),

Brindle (1987a) and others in recognising the Pygidicranoidea as a superfamily. Popham (1985) recognised their distinctness from the Forficuloidea and regarded them as an infraorder, Pygidicranida, comprising a single family within the Forficulina. Steinmann (1986) went further and proposed a new suborder, Catadermaptera, for the Pygidicranoidea and its relatives, other earwigs being placed in the suborder Endermaptera.

Sakai (1970–88) has published many works on the classification of the order based on modern techniques such as chromatography, laser technology, and morphometry; how useful these techniques are in an order notorious for convergence and parallelism remains to be seen. These works (see Sakai 1982 for additional references) are valuable compendia of the literature of the order. Steinmann (1975, 1978, for example) has produced many papers on earwig classification mostly with relatively minor variations following more traditional arrangements of the families, though he makes a major departure in his latest work (Steinmann 1986). In view of the lack of agreement among workers, the more conservative classification of Günther and Herter (1974), with corrected family-group nomenclature after Vickery and Kevan (1983), is followed here.

Key to the Higher Taxa of Dermaptera Known in Australia

- 1. Body normally distinctly hairy or strongly setose, not finely pubescent or glabrous; neck region not collar-like, anterior ventral cervical sclerite larger than posterior one; tegmina and hind wings usually present in adult; femora often compressed and keeled; ♂ forceps often asymmetrical, nymphs sometimes with multiarticulate cerci; ♀ usually with discernible genitalia (Fig. 23.5A); ♂ genitalia* with both medial lobes present, bent forward at rest, rarely with one lobe somewhat reduced, lateral lobes usually with teeth or processes **Pygidicranidae.**
- 2. Body normally glabrous, often shiny, or at most finely pubescent, sometimes quite strongly punctate; neck region with a 'collar', anterior ventral cervical sclerite smaller than posterior one; tegmina and/or hind wings often absent in adult; femora not compressed or keeled; ♂ forceps seldom asymmetrical, nymphal cerci not multiarticulate; ♀ without readily discernible genitalia (e.g. Fig. 23.5B); ♂ genitalia with at least one medial lobe permanently directed backwards, lateral lobes without teeth or processes 4
- 2(1). With 2 large, divergent tubercles, each overlying the base of one of the forceps **BLANDICINAE**
- Without such tubercles 3
- 3(2). Body more elongate, hairy but without stiff setae; femora keeled; terminal abdominal tergum longer than wide;

- forceps stout, more or less straight, nearly contiguous basally, asymmetrical in some genera PYGIDICRANINAE
 Body shorter and stouter with dorsal, bristle-like setae; femora not keeled; terminal abdominal tergum wider than long; forceps gently curved, distinctly separated basally ECHINOSOMATINAE
- 4(1). Tarsi with 2nd segment subcylindrical, not projecting beneath 3rd, which, in lateral view, arises more or less terminally from 2nd (Fig. 23.7A) 5
 Tarsi with 2nd segment often expanded laterally, projecting beneath 3rd (Figs 23.7B, C), or if not so, 3rd segment arising subterminally and more or less dorsally from 2nd 10
- 5(4). Usually wingless; pygidium distinguishable but concealed by being bent downwards between forceps; ♂ genitalia with 2 medial lobes, one of them (non-functional) flexed forwards, sometimes reduced **Anisolabididae**. 6
 Usually winged (or at least with tegmina); pygidium distinctly visible (though other 'opisthomeres' reduced); ♂ genitalia with only one medial lobe **Spongiphoridae**. 8
- 6(5). Body minutely pubescent, not strongly flattened; antennae elongate; thoracic mesonotum with posterior margin convex; forceps not long and slender, often asymmetrical in ♂♂; ♂ genitalia with manubrium at least as long as subgenital plate ANISOLABIDINAE
 Without above combination of characters; thoracic mesonotum with posterior margin more or less straight 7
- 7(6). Last abdominal tergum with posterior margin more or less straight ISOLABELLINAE
 Last abdominal tergum with posterior margin concave ISOLABIDINAE
- 8(5). Tegmina smooth, with lateral keels NESOGASTRINAE
 Tegmina punctate, without lateral keels 9
- 9(8). Head narrow, not transverse; eyes relatively small; antennae with 3rd segment shorter than 5th LABIINAE
 Head broad, transverse; eyes large and prominent; antennae with 3rd segment not shorter than 5th SPONGIPHORINAE
- 10(4). Tarsi with 2nd segment almost cylindrical (cf. Fig. 23.7A but 3rd segment arising subterminally and more or less dorsally); pygidium always directed downwards; ♂ genitalia with 2 medial lobes, 1 directed forwards, the other backwards 11
 Tarsi with 2nd segment produced or expanded (Figs 23.7B, C); pygidium not directed downwards; ♂ genitalia with only one medial lobe 12
- 11(10). Body extraordinarily flattened and often contrastingly pigmented **Apachyidae**
 Body and coloration not as above **Labiduridae**
- 12(10). Tarsi with 2nd segment produced below 3rd but not expanded laterally (Fig. 23.7B) **Chelisochidae**
 Tarsi with 2nd segment produced below 3rd and expanded laterally (Fig. 23.7C) **Forficulidae**

* The sexes can be distinguished by counting the ventral abdominal sclerites; but in both sexes the plate of the first metameric segment is wanting. Thus in males the large triangular terminal subgenital plate is number 9 (Fig. 23.1B) whereas in females it is number 7 (Fig. 23.3B), because of reduction of segments 8 and 9 (see p. 361). The male genitalia (Fig. 23.4) are conspicuous in the mid line above the subgenital plate. In females the ovipositor, also above the subgenital plate, is very much reduced except in most Pygidicranidae (Fig. 23.5 and p. 362). Males of most species have heavier and better developed forceps than females. *Note*: All nymphs (except most Pygidicranidae) have female-type forceps with the male-type abdominal sclerite arrangement.

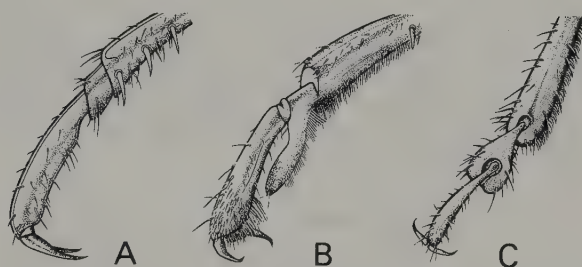


Fig. 23.7 Tarsi: A, Spongiphoridae; B, Chelisochidae; C, Forficulidae.

[T. Nolan]

Superfamily PYGIDICRANOIDEA

1. Pygidicranidae. Considered to be the most primitive family of living Dermaptera; its members are not common. They are 10–35 mm in length, light to dark brown, winged and have long antennae. The PYGIDICRANINAE (*Cranopygia*, Fig. 23.8A; *Dacnodes*) are slender and smooth, whereas ECHINOSOMATINAE (*Echinosoma*) are stout and covered with short bristles. The most recent

treatment of this group is that of Steinmann (1986). Brindle (1987b) described *Austroblandex bituberculatus* (BLANDICINAE) from Vic. The other 3 blandicine genera are from South Africa and Madagascar. With *Dacnodes* and *Echinosoma* both represented in Australia and South Africa, *Austroblandex* further indicates the Gondwanan affinities of the family.

Superfamily ANISOLABIDOIDEA

2. Anisolabididae (= *Carcinophoridae* *auctt.*). The Anisolabididae, regarded as constituting a superfamily of their own (Anisolabi[d]oidea) by Sakai (1982 *et seq.*), consist of wingless species having the manubrium at least as long as the subgenital plate. In the ANISOLABIDINAE, *Titanolabis* has the meso- and metasternum lobed posteriorly. The abdomen of *Anisolabis* is weakly dilated, but that of each of the closely related genera *Gonolabis*, *Mongolabis* and *Notolabis* is noticeably broadest towards the apex; these genera may also be distinguished by the male genitalia. *Titanolabis colosseae* (Fig. 23.8B) is a very large and robust earwig, with some specimens attaining

55 mm. It is reddish brown to black and is found in rainforests and wet sclerophyll forests of eastern Australia. All ISOLABIDINAE (= Brachylabidinae, Brachylabinae auctt.) are apterous, dull, dark brown to black, often thickly clothed with fine bristles, and have short antennae. *Antisolabis*, *Brachylabis* and *Nannisolabis* may be separated by the lateral keel of the mesonotum and the form of the proximal antennal segments. The ISOLABELLINAE (Parisolabidinae) superficially resemble the Isolabidinae. *Parisolabis* is the only known Australian genus. *Euborellia annulipes* is cosmopolitan.

3. Labiduridae. This cosmopolitan family of handsome earwigs is well represented in Australia. Many species are reddish brown and apterous. They range from 10–45 mm long as adults and are found throughout Australia. Sakai (1970), Günther and Herter (1974) and Steinmann (1977) have provided revisions of the group. LABIDURINAE are winged and somewhat glossy, have long antennae (more than 20 segments), and are often fairly large. *Labidura truncata* is a large, long-legged, mostly pale species having the ecdysial suture obsolete. It occurs throughout Australia, especially in sandy habitats. It is up to about 35 mm long and dull brown with straw-coloured markings. The male has long, slender forceps, widely spaced basally, with a prominent tooth near the middle of the inner edge. Specimens from northern Australia seem darker than those from more southern regions. *Nala lividipes* is common throughout Australia; in Qld and north-western Australia, it has been reported feeding on seedlings of field crops and is often attracted to lights.

Superfamily APACHYOIDEA

4. Apachyidae (Plate 2, E) are large and strikingly pigmented and very flattened for their existence under bark.

Four species of *Apachyus* occur on the eastern coastal plains and tablelands in rainforest and wet sclerophyll forests. They are treated as a separate family by Sakai (1982, 1987) and superfamily by Sakai (1982).

Superfamily FORFICULOIDEA

5. Spongiphoridae (= Labiidae auctt.). This large, widespread family is poorly represented in Australia. All known species are winged, glossy brown to black, and small (usually under 15 mm in length). They never seem to be common, but have been collected principally on the eastern tablelands and coast. The LABIINAE are represented by *Chaetospania* (Fig. 23.8C), which is decidedly flattened and has the posterior margin of the head subsinuate, and *Labia*, which has the head truncate posteriorly. The SPONGIPHORINAE have a broad head and very large eyes. *Apovostox* and *Marava* are very similar and separated reliably only by the male genitalia. *Nesogaster* is the only known representative genus of the NESOGASTRINAE.

6. Chelisochidae. This is a small, mainly tropical family with CHELISOCHINAE represented in northern Australia by dark brown to black earwigs ranging from 15–25 mm long. They are commonly encountered among the tightly overlapping leaf bases of *Pandanus* where they are afforded protection during the day. *Hamaxas* is small, and has pubescent legs with tibiae smooth above. *Chelisoches* (Fig. 23.8D) is larger, robust and the tibiae are flattened and sulcate above. *C. morio* is synanthropic and widely distributed throughout the Pacific and elsewhere. *Proreus* is similar to *Chelisoches*, but more slender, and has slender antennae; *Lamprophorella* has a strongly depressed body.

7. Forficulidae. This large, cosmopolitan family is poorly represented in Australia by a single subfamily,

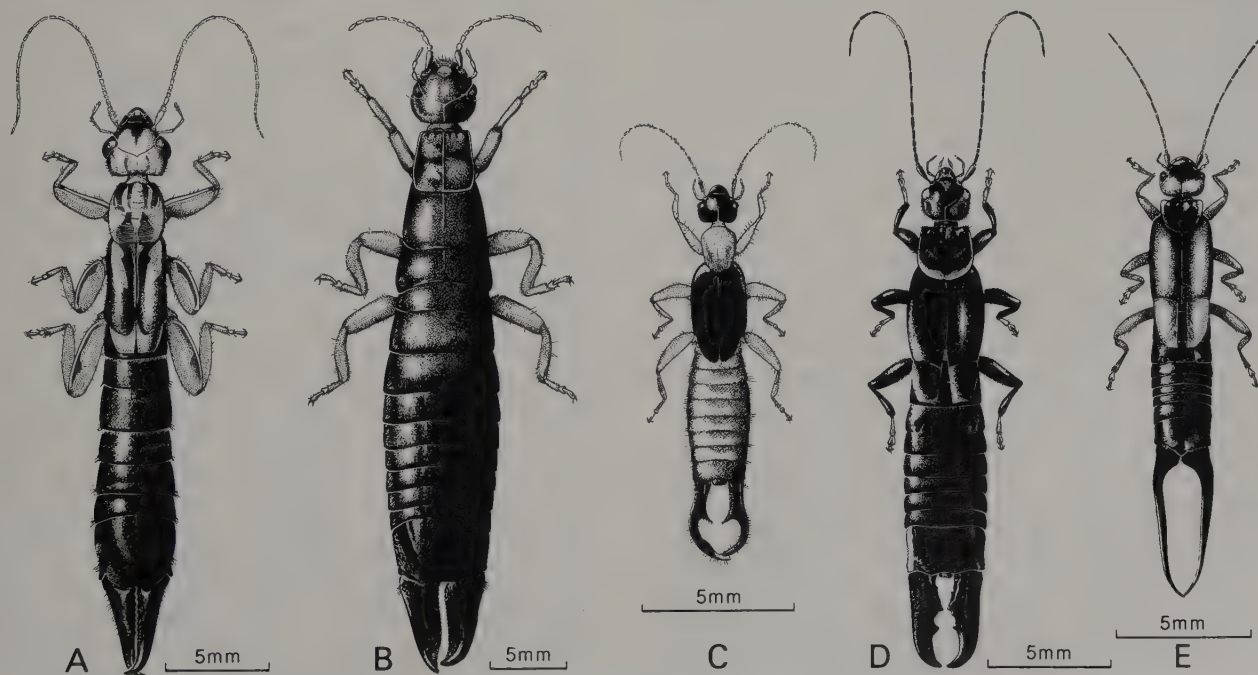


Fig. 23.8 A, *Cranopygia daemeli*, Pygidicranidae, ♀; B, *Titanolabis colossea*, Anisolabididae, ♂; C, *Chaetospania brunneri*, Spongiphoridae, ♂; D, *Chelisoches morio*, Chelisochidae, ♂; E, *Elaunon bipartitus*, Forficulidae, ♂.

[T. Nolan]

FORFICULINAE. All known species are winged as adults, brownish in colour and range from 15–25 mm long. *Doru* and *Elaunon* (Fig. 23.8E) have the abdomen parallel in outline, and the pygidium of *Doru* bears a spine. *Forficula*, represented by two species, has the abdomen broadest in the middle and the forceps depressed and

basally dilated. *F. auricularia*, the European earwig, now dispersed virtually world-wide in temperate regions, can be a nuisance in gardens (see p. 364).

ACKNOWLEDGMENTS. The authors would like to thank Drs G. Cassis and S. Sakai for helpful comments.

Orthoptera*

(*Grasshoppers, locusts, katydids, crickets*)

D. C. F. RENTZ

Mandibulate, exopterygote Neoptera, having the hind legs usually saltatorial, with the hind coxae nearly always small and well separated; pronotum with large descending lateral lobes; wing rudiments of nymph reversing their orientation in the later instars.

The Orthoptera comprise the terrestrial insects commonly known as short-horned grasshoppers, katydids, locusts (in the strict sense: not the cicadas) and crickets, as well as related groups without common names. They are mainly medium-sized to large and include some of the largest living insects, with bodies over 11.5 cm long and wingspans more than 22 cm. They occur over all but the coldest parts of the earth's surface, but are best developed in the tropics. They are often abundant as individuals, forming a characteristic and striking component of the fauna in many parts of the world. The order is perhaps best known for the power of jumping possessed by nearly all species, and for the 'singing' that many indulge in, especially at night. The word locust has become a byword for the devastation caused by their migrating swarms. They are mentioned in biblical writings and early Chinese literature, while in the present century they have provoked one of the most massive concentrations of research ever achieved in the field of entomology. Biological types represented in the Orthoptera include phytophilous, geophilous, cavernicolous, myrmecophilous and burrowing; diurnal and nocturnal; vegetarian and carnivorous. More than 20 000 species are known. Comprehensive accounts of the order are given by Chopard (1938, 1949b), Beier (1955) and Kevan (1982).

Anatomy of Adult

Head. Typically hypognathous, usually inserted to some extent into the pronotum, anterior part of vertex often projecting forward beyond the eyes to form a *fastigium*, face then usually reflexed; sometimes the whole of the anterior part of the head has a strongly projecting, elongate-conical form. Antennae short to several times as long as the body, with from 7 to very many segments; greatly reduced in a few burrowing forms. Slifer (1974) and Slifer *et al.* (1957, 1959) have studied the sense organs on the antennae of Orthoptera. Eyes usually of medium to large size, but strongly reduced or absent in some cavernicolous and subterranean forms. Ocelli usually 3, sometimes fewer or absent. Mandibles large, somewhat asymmetrical, in predacious forms more slender and pointed, in phytophagous forms with broad grinding surfaces; exceptionally, but often only in the male, they may be grotesquely enlarged, rarely modified for stridulation (Figs 24.5D, 6F). Maxillae with 5- or rarely 6-segmented palp, large galea, and toothed lacinia; maxillary palp in at least 1 group modified for stridulation (Fig. 24.5A). Labium with 3-segmented palp and large paraglossae; glossae reduced or absent. Hypopharynx present.

Thorax. Prothorax large, usually capable of only limited movement on the mesothorax. Pronotum nearly always larger than the other nota, with large descending lateral lobes, which are usually subvertical and form the sides of

* Some parts of this chapter are from Key (1970).

the prothorax. Often the free margins of the pronotum are formed by a fold projecting beyond the lines of articulation with adjacent sclerites, especially posteriorly, where a broad extension commonly covers the wing bases. In a few burrowing forms the lateral lobes curve ventrally, even meeting on the mid-ventral line. Spines, crests or foliaceous outgrowths, some of which evidently have a cryptic significance, are sometimes developed. Prosternum sclerotised, very variably constructed; propleural sclerites often vestigial, at most their ventral extremities visible below the pronotum. Meso- and metathorax similar, rigidly connected, the latter usually the larger; the sterna sclerotised, usually broad, comprised principally of a large basisternum to which a smaller sternellum is partly fused; pleura well developed, similar, usually somewhat oblique, episternum and epimeron subequal. Meso- and meta-thoracic spiracles present.

Legs. Fore and mid legs usually similar and gressorial, but some predacious forms have fore legs provided with

rows of spines on ventral sides of femur and tibia which may be raptorial; fore legs of burrowing forms sometimes highly modified for digging. Hind legs nearly always modified for jumping, larger than the others, the femur thickened to accommodate powerful muscles, and the tibia provided distally with articulated spurs; occasionally they may be further adapted for life on sand by enlargement of the tibial spurs, for swimming by a broadening and flattening of the tibia and tarsus, or for movement on water surfaces by the development of long, hairy spines on the tibia. Coxae of hind legs nearly always small and well separated. Tarsi 1–4-segmented, nearly always with a pair of terminal claws and usually with an arolium. Fore tibia of most Ensifera bearing an auditory tympanal organ near the base on one or both sides, the tympanum being exposed, or largely concealed by an integumental fold. Hind femur of some species equipped on its inner face with a ridge, or row of minute pegs, that plays a part in stridulation (Figs 24.6A–D).

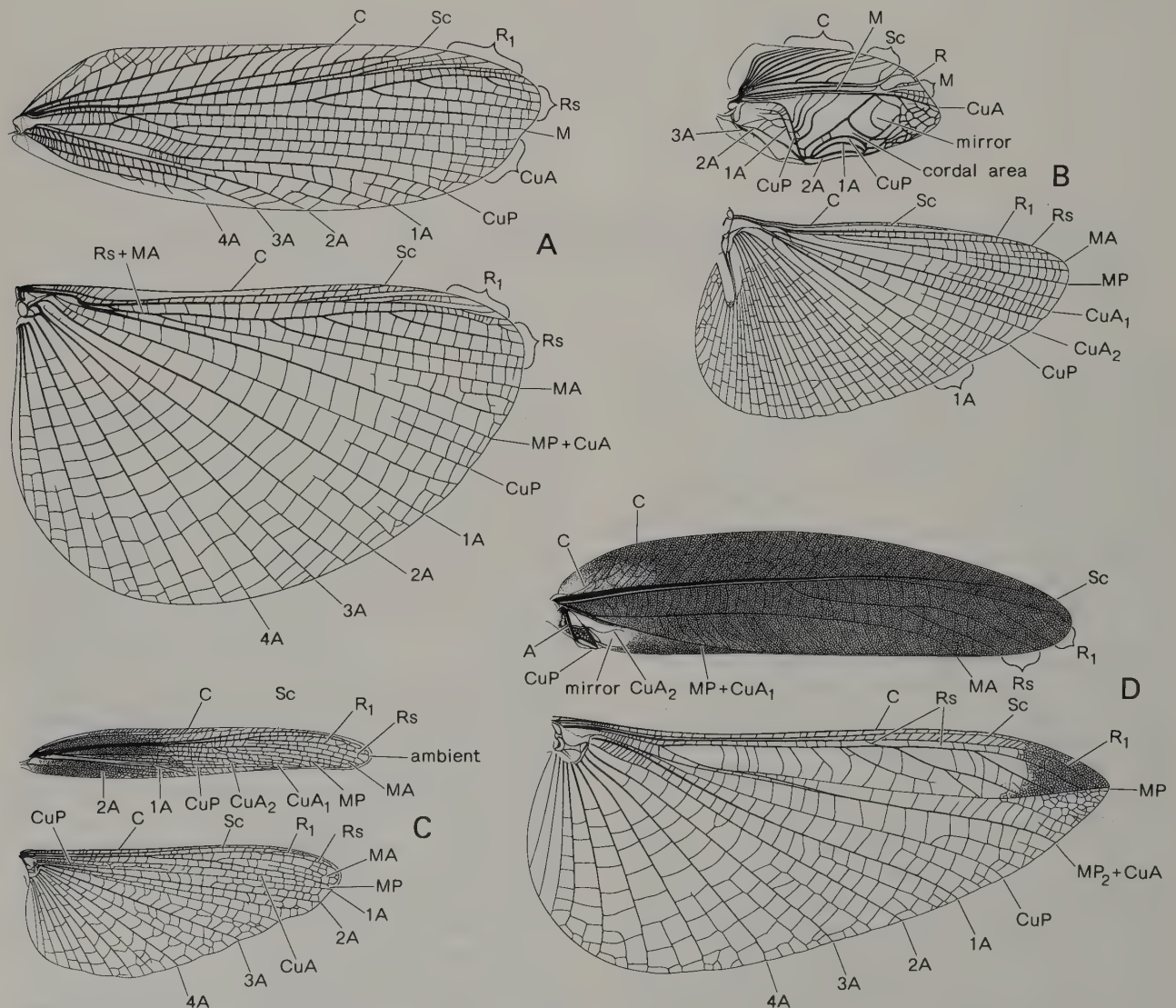


Fig. 24.1 Male wings: A, *Hadrogyllacris* sp., Gryllacrididae; B, *Teleogryllus commodus*, Gryllidae; C, *Bermius brachycerus*, Acrididae; D, *Torbia viridissima*, Tettigoniidae. [F. Nanninga]



Fig. 24.2 *Chortoicetes terminifera*, Acrididae, last nymphal instar. Note exposed hind wing in this nymph as opposed to the exposed fore wing of the brachypterous adult in Fig. 24.14a. [F. Nanninga]

Wings. Most Orthoptera are fully winged in both sexes, but brachypterous or apterous forms are numerous in all of the larger families, and some families are apterous throughout. Reduction usually affects both fore and hind wings; occasionally the hind wings may be lost, but the fore wings are unaffected; and in two superfamilies the fore wings are always reduced, even when the hind wings are fully developed. Commonly the female is affected more than the male, rarely vice versa; the male may be fully winged and the female apterous. Reduction may be arrested when just enough of the fore wing remains to permit the performance of secondary functions, e.g., stridulation in Ensifera and others (Figs 24.3, 4, 5E, F), protection of the abdominal tympanal organ in Acridoidea.

When fully developed, fore wings usually narrow, toughened, in the closed position overlying the hind wings along the abdomen and overlapping across the mid-line; sometimes broader and modified to resemble leaves. Hind wings broad, largely or wholly membranous, with a large anal area; in repose folded fanwise, either throughout, or only in the anal or cubito-anal region. Venation (Ragge 1955a) very varied (cf. Fig. 24.1). C submarginal in the fore wing, at least towards the base, or absent, the more proximal part of the anterior wing margin unsupported, or strengthened by an ambient vein; in the hind wing marginal. MA usually present. Cu dividing near the wing base into CuA, often branched, and an almost always unbranched CuP. Anals numerous in the hind wing. Cross-veins and intercalary veins are generally present and an archdictyon may occur over part or all of the fore wing. The venation of the fore wing, and less often of the hind wing, may show a variety of stridulatory modifications often restricted to, or better developed in, the male (Figs 24.3, 4).

Abdomen. Consists of 11 segments; usually smooth, but sometimes sculptured in brachypterous and apterous species. T9 and T10 of male sometimes bear integumental outgrowths, some proximal terga modified for stridulation in some Ensifera; T11 forms the supra-anal plate, which is sometimes fused with T10. Sterna fully sclerotised, or represented by sternites and laterosternites surrounded by membrane; S1 often closely associated with the metathoracic sternum; S11 represented by the paraprocts. Cerci usually unsegmented, of varied length, usually larger in male, where they may be modified as clasping organs. Spiracles present on segments 1 to 8. Sometimes one of

the anterior terga bears a series of stridulatory ridges laterally. In most Acridoidea T1 bears a conspicuous lateral tympanal organ, which is covered by the fore wing except in flight.

The male terminalia have been described by Snodgrass (1937). S9 (or part of it) forms the subgenital plate (S8 in Tridactyloidea), which sometimes has a pair of styles, or is provided with a posterior lobe, which may be elongate or otherwise modified. S10 concealed. The genitalia, concealed by the subgenital plate, are diversely constructed, often largely sclerotised, phallic and periphallic structures of uncertain homology; they are often useful in classification.

In the female, the subgenital plate is formed by S8 or S9; S10 (or S9 and S10) reduced and concealed. The ovipositor (sometimes obsolete) comprises 3 pairs of valves, of which the inner pair may be greatly reduced. It may consist of an ensiform or cylindrical tube (most Ensifera), formed by the tongue-and-groove articulation of 2 or all of the valves and sometimes exceeding the rest of the body in length; or of a dorsal and ventral pair of free prongs, representing the anterior and posterior valves, hinged at their base and capable of being approximated and separated like jaws (most Caelifera).

Internal Anatomy. Alimentary canal straight or convoluted, with a large crop, variably developed gizzard, and mid gut with 2 to 6 caeca anteriorly. Salivary glands variably developed. Malpighian tubules numerous, entering the gut separately or by one or more common trunks. The central nervous system includes 3 thoracic and 3–7 discrete abdominal ganglia. The male reproductive organs comprise a pair of testes, discrete or fused, connected to the ejaculatory duct by paired, simple or epididymis-like vasa deferentia; tubular accessory glands open into the duct, usually a pair of vesiculae seminales, and, in the Ensifera, paired or unpaired globular 'prostate' glands. In the female, the ovaries comprise a number of panoistic ovarioles, arranged serially along the lateral oviducts or arising in a cluster; the lateral oviducts join to form a short common oviduct, or occasionally open independently into the genital atrium, as does the paired, or usually unpaired spermatheca. Accessory glands open at the base of the ovipositor in some Ensifera, while in most Caelifera the anterior extremities of the oviducts are glandular and secrete the material that goes to form the egg pod. In some acridids a pair of 'Comstock-Kellogg' glands, thought to produce a sex-attractant substance, open into the genital atrium. Many Orthoptera possess integumental glands, of the most diverse types and location, from which repugnatorial fluids may be released, while similar glands in males of some species have a sex-attractant secretion. Important work on the morphology of the spermatozoa of orthopteroid insects was presented by Baccetti (1987b).

Karyotype. The chromosome set has $2n \delta$ ranging from 8 to 57 in the species studied (M. J. D. White 1951), while $2n = 68$ in the parthenogenetic tetraploid *Saga pedo* (Tettigoniidae); supernumerary chromosomes sometimes occur. The chromosome number and morphology are almost constant throughout some large groups, but highly

diversified in others. Sometimes the karyotype affords the best specific characters and may reveal the existence of sibling species; intraspecific chromosomal polymorphisms and chromosome races are also common. The male is usually XO, but XY and X_1X_2Y sex mechanisms also occur.

Immature Stages

Egg. The eggs may be oval, elliptical or cylindrical, sometimes curved, and sometimes strongly flattened; shell thin, pale and smooth, or thick, pigmented and minutely sculptured, either apex or both rarely with a 'plug'.

Nymph. The newly-hatched young is enclosed in the embryonic cuticle, i.e. it is a 'pronymph' or 'vermiform larva'. At hatching, according to Bernays (1972b), the egg shell is fractured by pulsations of an extrusible *cervical ampulla* in the dorsal membrane of the neck, usually assisted by the cutting action of a ridge, or row of teeth, situated on the front of the head. The ampulla also plays a part in the emergence of the pronymph from the egg repository in soil or plant tissue, and in the 'intermediate moult', discussed by Bernays (1972a), by which the embryonic cuticle is cast immediately the insect is freed. The nymph differs from the adult mainly in the rudimentary reproductive organs and wings (in species possessing

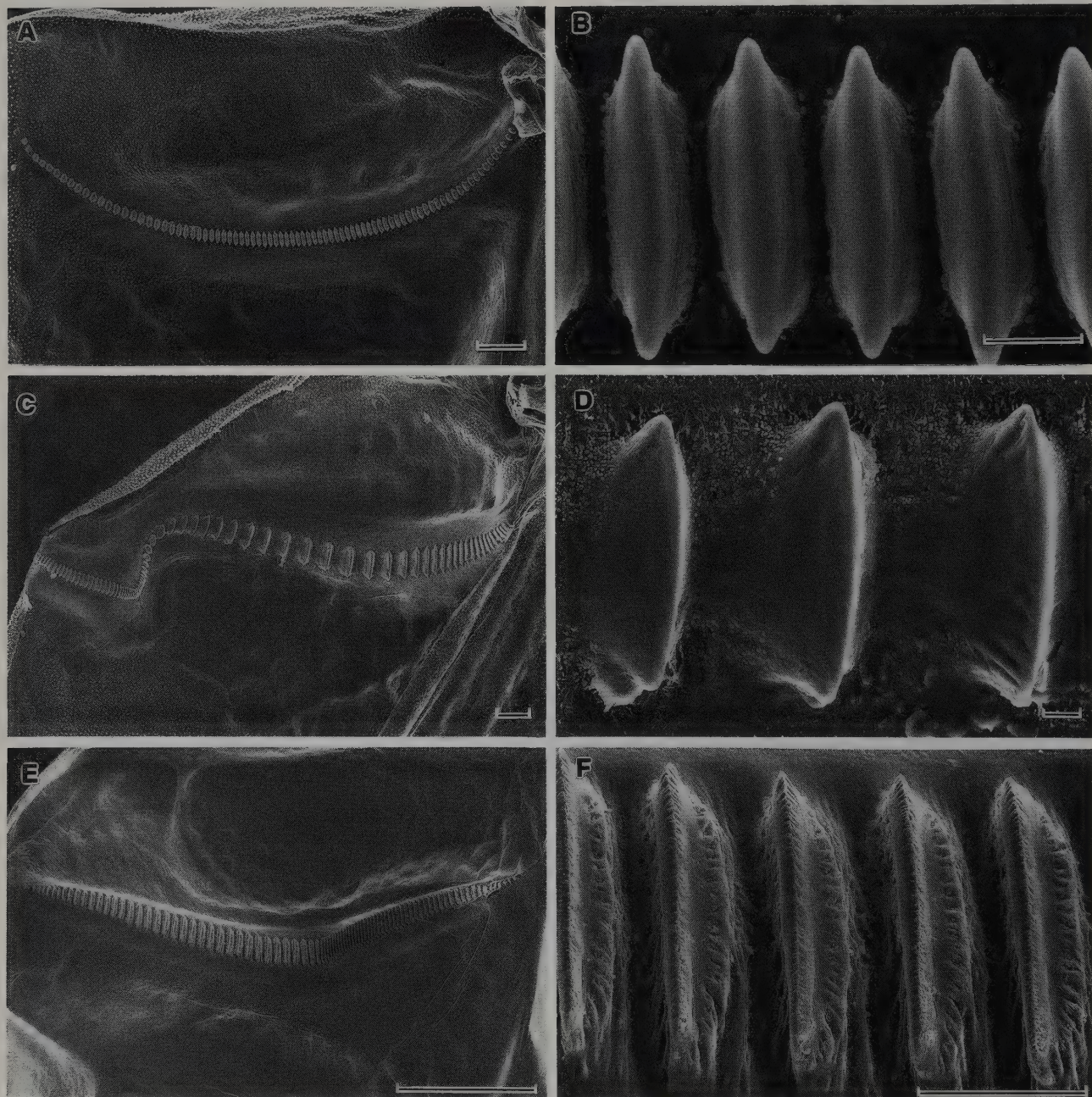


Fig. 24.3 Stridulatory files on the underside of the tegmen of some Tettigoniidae. A, C, E file, B, D, F enlargement of some teeth in middle of same; A, B, *Oligodectoides tindalei*, Tettigoniinae; C, D, *Phaneroptera gracilis*, Phaneropterinae; E, F, *Acripeza reticulata*, Phaneropterinae. Scales: A, C, F = 100 μ m; B, D = 10 μ m; E = 1 mm.

[K. Pickerd]

them), in the less elaborated pronotum, and usually in the smaller number of antennal segments. It undergoes several moults (usually fewer in the male than the female), which usually take place in an inverted position from some support, the cervical ampulla again coming into play in rupturing the old cuticle. The wing rudiments and terminalia increase in size from instar to instar. The former are initially lateral in position, with the costal margin ventral, as in the adult, but at one of the later ecdyses—usually the antepenultimate one—they rotate about their basal attachment and assume a reversed, more dorsal position, in which the costal margin is dorsal, the morphologically ventral surface external, and the hind wing overlaps the fore wing (Fig. 24.2). The number of antennal segments may increase by progressive division.

Biology

Orthoptera are solitary or sometimes gregarious, mostly active insects, usually progressing by walking, but capable of powerful jumps. Jumping occurs usually as part of the escape reaction, or as a means of launching the insect for flight. In some small groups the capacity for jumping has been largely or wholly lost. Flight may be weak and of a fluttering or blundering type, or powerful and sustained, leading to extensive migrations.

Song. Song in orthopteroid insects is a characteristic element in behaviour. The sounds produced, as well as the

mechanisms involved, are highly diversified (Figs 24.3–6) (Busnel 1955). The sounds are usually produced by males. In ensiferous Orthoptera, katydids and crickets sing by rubbing modified portions of the fore wings together. In the right wing of tettigoniids a posterior branch of CuA bends towards the posterior margin in the proximal region of the wing and divides to form the anterior and posterior borders of a usually membranous area, the 'mirror', whose proximal border is formed by CuP, likewise reflexed. In the left wing these veins take a corresponding course but, in addition, CuP is raised and serrulate on its underside forming the 'file', which in stridulation is scraped over the raised posterior portion of the right wing, the 'scraper' (Figs 24.3, 4). In gryllids the situation is reversed, the right wing is positioned over the left. Females of some species, especially the Phaneropterinae (Tettigoniidae), also stridulate by rubbing their wings together but this involves other veins, especially along the dorsal margins of the tegmina.

The song is produced generally only on the closing stroke of the fore wing. The sound produced by a single stroke of the fore wing is called a 'pulse'. Each pulse consists of a number of individual tooth strikes of the scraper on the file. The 'pulse rate' in a given insect varies with temperature; the higher the temperature, the faster the pulse rate. This can vary from 4 or 5 per second to over 200 per second. The songs of different species differ in

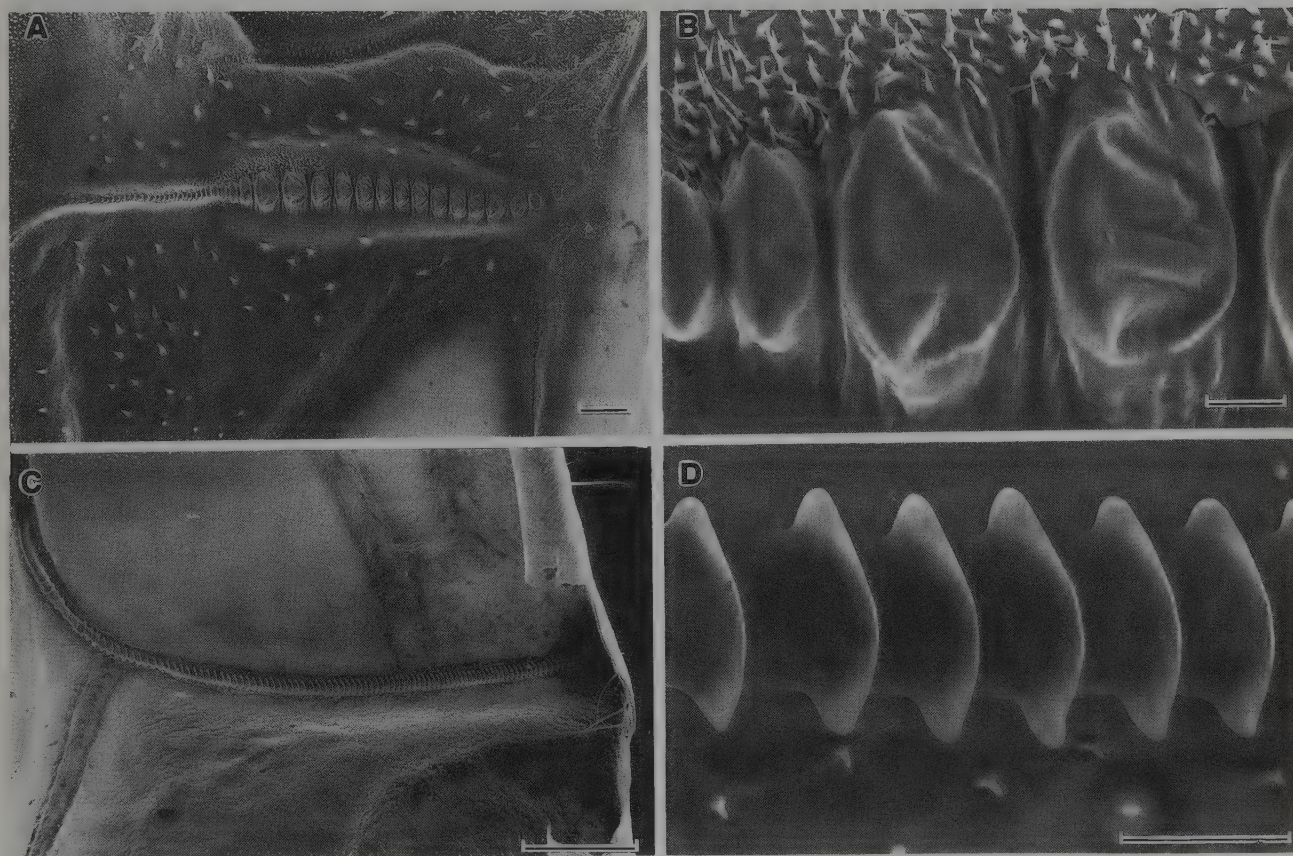


Fig. 24.4 Stridulatory files on the underside of the tegmen in ensiferous Orthoptera. A,C file; B,D enlargement of some teeth in middle of same; A, B, *Conocephalus albescens*, Conocephalinae-Tettigoniidae; C, D, *Pteronemobius nundra*, Nemobiinae-Gryllidae. Scales: A = 100 μ m; B = 20 μ m; C, D = 10 μ m. [K. Pickerd]

the character of the pulses, pulse rate and the way the pulses are grouped. Pulses produced by crickets are relatively musical in quality and usually have a definite pitch. This varies in crickets from around 1500 to 10 000 Hz and corresponds to the tooth strike rate. Katydid songs are noisier and contain a wide range of frequencies and usually cannot be assigned a definite pitch. Frequencies in katydids range from 20 000 to 100 000 Hz and may be quite inaudible to some persons, especially older individuals.

Band-winged, acridid grasshoppers (often placed in the Oedipodinae (= Locustinae) but here considered as part of

the Acridinae) 'crepitate' by snapping their hind wings alone (Fig. 24.6E) or in conjunction with the fore wings in flight. The sound is like a crackle or buzz. Some grasshoppers (the Gomphocerinae, primarily, which are not represented in Australia) stridulate by rubbing the hind femora against the outer surface of the fore wings, producing a soft, raspy sound; the hind femora are endowed with a series of pegs which function similarly to the file described above.

Most singing Orthoptera are capable of producing several types of songs which are produced under different conditions. Generally the loudest and most commonly

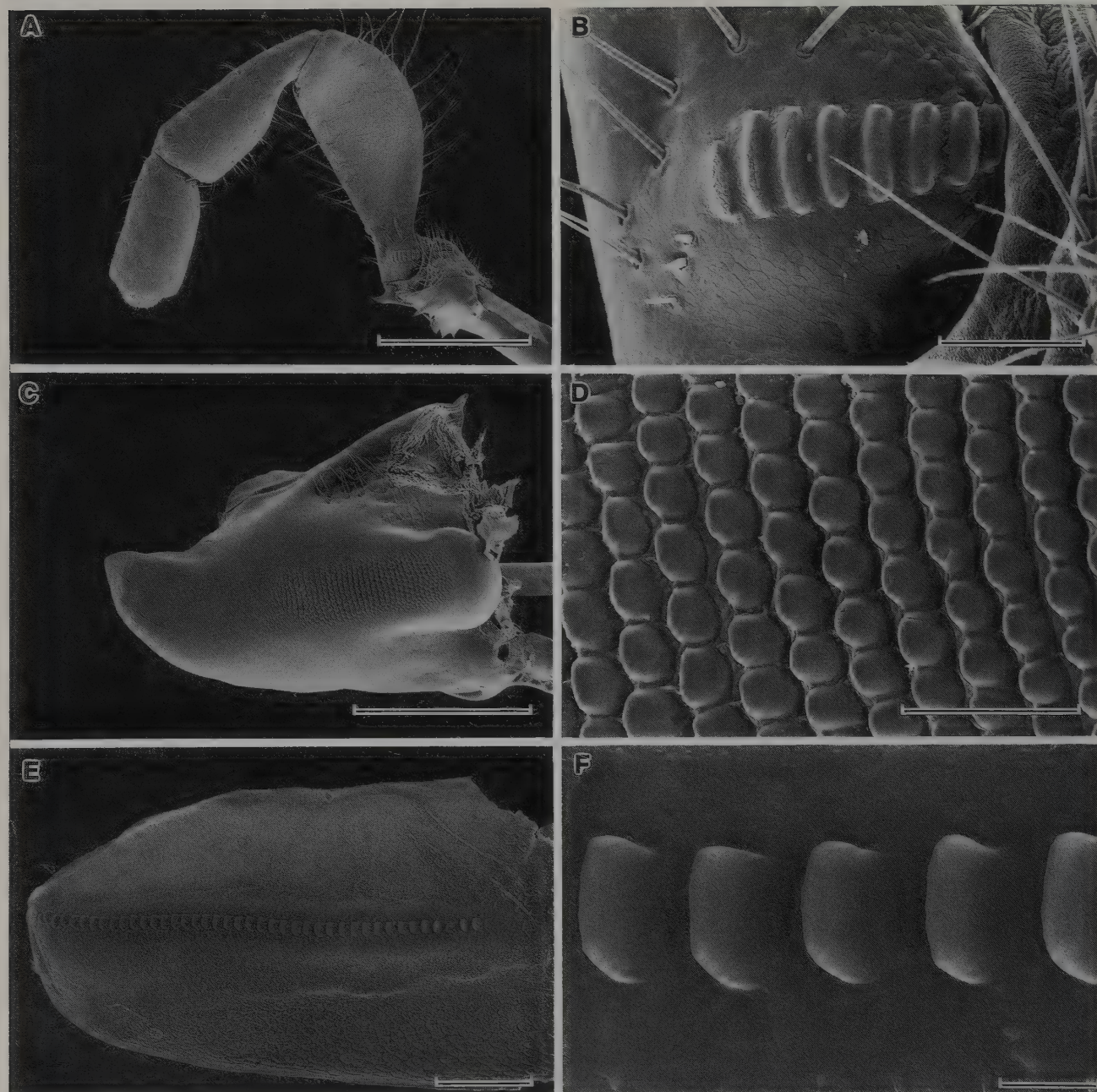


Fig. 24.5 Stridulatory mechanisms in some unusual Orthoptera. A–D, *Cyllindracheta psammophila*, Cyllindrachetidae, A, maxillary palp with stridulatory file at base, B, enlargement of same; C, mandible with stridulatory area at base, D, enlargement of same; E, F, *Tridactylus m. mutus*, Tridactylidae, E, tegminal stridulatory file, F, enlargement of same. Scales: A, C = 1 mm; B, D, E = 100 μ m; F = 10 μ m.

[K. Pickerd, E. Hines]

encountered song is the 'calling song' which is uttered by the male to attract females for mating. 'Fighting' or 'aggressive' songs, produced largely by male crickets in the presence of other males, determine the dominance of an individual. Courtship songs are produced by a male in the presence of a female. These sounds are usually very low and not broadcast to avoid attracting other individuals. Many Orthoptera produce 'alarm' or 'disturbance' calls when threatened or handled. Many Australian grasshoppers such as *Ecphantus quadrilobus* rub the mandibles together (Fig. 24.6F) to produce a squeaking sound when seized. Some katydids make similar sounds

and others, including females, produce an alarm sound by rubbing the fore wings together.

In general, grasshoppers sing during daytime, katydids sing at night and crickets sing both day and night. There are a great many exceptions, of course. The cone-headed katydids in the Copiphorini often chorus at dusk, that is, two or more individuals sing simultaneously, their pulses synchronised, producing an irritating, pulsating sound. The songs produced are nearly always characteristic for the species; often they appear to constitute the principal isolating mechanism between closely related species and may provide the best taxonomic characters for separating

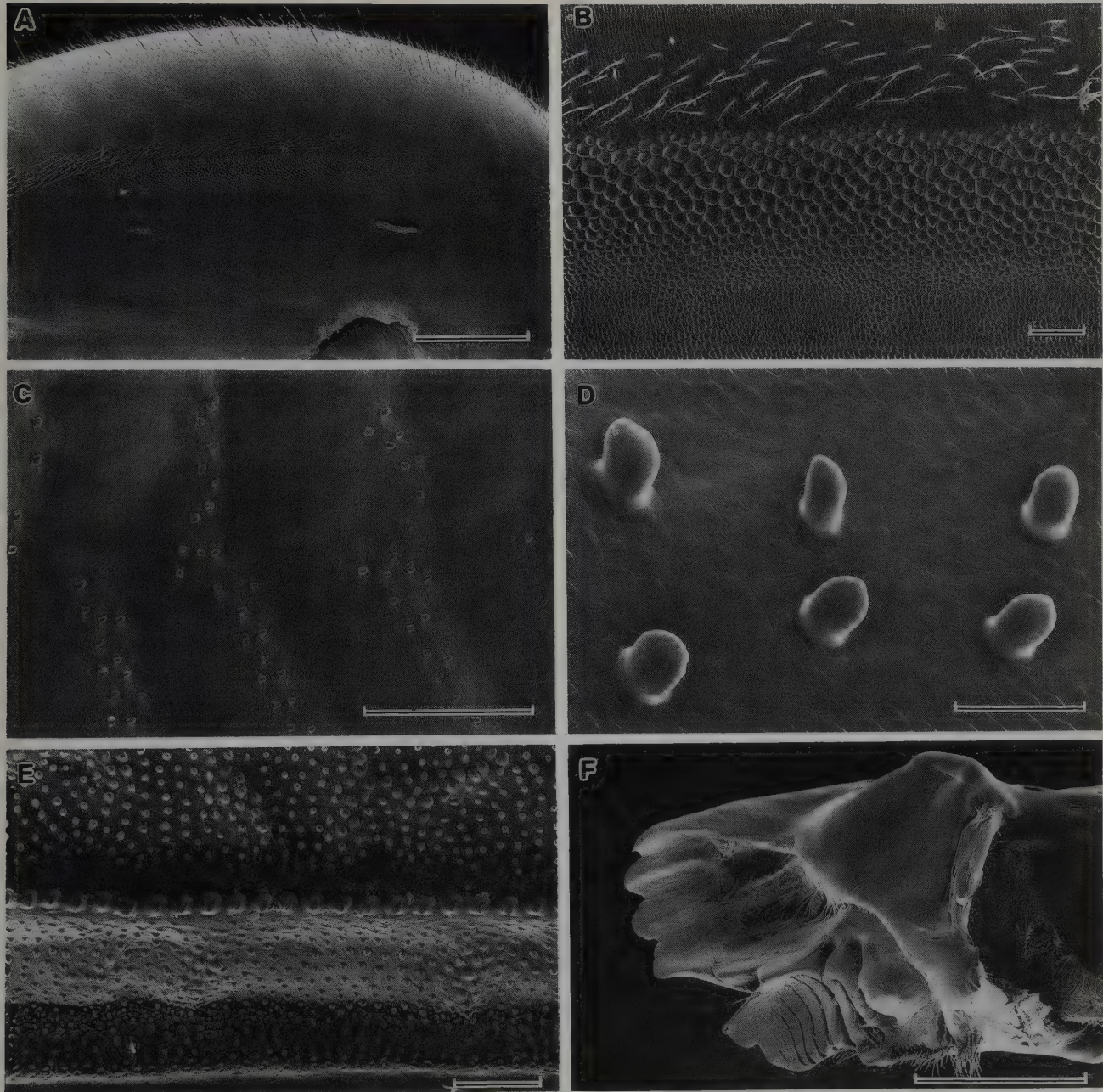


Fig. 24.6 Stridulatory mechanisms in a variety of Orthoptera. A, B, *Xanthogryllacris punctipennis*, Gryllacrididae, A, inner surface of hind femur illustrating stridulatory area, B, enlargement of same; C, D, *Penalva* sp., Stenopelmatidae, C, stridulatory pegs on inner surface of hind femur, D, enlargement of same; E, *Sphingonotus erythropterus*, Acrididae, intercalary vein of tegmen; F, *Ecphantus quadrilobus*, Acrididae mandible with cusp showing ridges which apparently are sound producing. Scales: A, F = 1 mm; B–E = 100 μ m.

[K. Pickerd]

them (Bailey 1979; Otte and Alexander 1983; Rentz 1985). It has been shown that crepitation in flight, which is often associated with a dazzle display of coloured hind wings, or with a zig-zag flight path, probably serves to disorient bird predators (see Cott 1940).

Behaviour. Orthoptera have been popular subjects for the behaviourist. Much has been done of an interdisciplinary nature relating to speciation and natural selection (see R. D. Alexander 1960, 1962, 1967 review article, 1969). Alexander and Otte (1967) made comparative studies of the structure of cricket genitalia and their role in copulation. Gwynne (1981, 1982, 1984a-c) and Thornhill and Gwynne (1986) have studied sexual selection among katydids and the multiple uses of the spermatophore. Otte (1970, 1972) made a comparative study among grasshoppers, the latter dealing with Australian species and comparing their behaviour with those from the Northern Hemisphere. Otte (1977) presented a treatise on orthopteran signalling systems. Kalmring and Elsnér's (1985) compendium on acoustic and vibrational communication used mostly orthopteran examples. Robinson (1968, 1969) reported on startle display and defensive displays of tropical American orthopteroid insects.

Many Orthoptera have excellent sight or hearing and are wary insects and difficult to approach. Others are sluggish, relying for protection upon cryptic or distasteful properties, or hiding in inaccessible places. If seized, almost all species will kick out with their usually spiny hind tibiae and regurgitate the acrid contents of the crop (see Lymbery and Bailey 1980); most large species will bite without hesitation and can draw blood. If the insect is seized by a hind leg, the leg will generally be lost between femur and trochanter, where there is an occlusive diaphragm. Various species, often aposematically patterned, will squirt or exude repugnatorial secretions from intersegmental (integumental) glands.

Most species are phytophagous, feeding especially on the foliage of higher plants, but some on roots, cryptogams or unicellular organisms ingested with mud. Others are omnivorous, while a few substantial groups are predacious on other insects, which they seize with their fore legs.

Species living in the open show elaborate cryptic resemblances to leaves, twigs, bark or stones. These resemblances (which primarily deceive vertebrate predators) involve structural modifications of various parts of the body, combined with camouflaging colours and patterns and with behaviour appropriate to these adaptations. Mimicry of other insects is also found. Aposematic colouring (Plate 2, H, L), associated with distasteful properties, sluggish behaviour, occupancy of conspicuous situations, and sometimes limited gregariousness, is not infrequent. Bright colours on parts of the body that are concealed at rest may be in the category of 'flash', or frightening colours (Plate 2, F); they are commonly different in related species and are much used by the taxonomist. A few species may bury themselves in sand for short periods, or overwinter in soil cracks or under litter, even though in general they live fully exposed lives. Some oxyines are semiaquatic, living on the hygrophilous

vegetation or damp soil fringing bodies of water (or even on floating plants) and swimming freely, or skating over the surface film; these commonly show limited structural adaptation for aquatic life (p. 391).

The cryptozoic forms lack bright colours and cryptic adaptations. They are mostly pale, drab or sometimes black insects, very smooth or with a short, velvety pile of hairs, and mostly more or less cylindrical or dorsoventrally compressed; fore legs or mandibles may be adapted for digging. Cavemicolous forms have drab pigmentation, smooth and thin integument, long and delicate appendages, and small eyes. The very few permanently subterranean species are pale, cylindrical, larviform creatures, with vestigial eyes, reduced antennae, non-saltatorial hind legs, and powerful, burrowing adaptations; or are small, depressed myrmecophiles.

Reproduction. Diverse attitudes are adopted in copulation (see Alexander and Otte 1967). The sperm are transferred in spermatophores, which vary greatly in size and complexity, but consist essentially of a vesicle, with a narrow opening usually situated at the end of a tubular extension. In the Ensifera a spermatophore is transferred at each copulation and the vesicle remains attached externally to the vulva; it may be eaten by the female and often serves an important nutritive function towards the development of the fertilised embryos (see Thornhill and Gwynne 1986). In the Acridoidea several small spermatophores may be inserted into the female tract, or the tubular part of a single spermatophore may penetrate the spermathecal duct, while the vesicle remains in the phallus. Blackith and Blackith (1967) state that morabine eumastacids produce no spermatophore and that sperm is delivered directly to the bursa copulatrix and not into the spermathecal duct.

The eggs are usually laid in the soil, but many Ensifera insert them into stems or leaves, and a few cement them in rows to twigs; a few Acridoidea lay in pithy stems, soft spots in dead timber, or grass tussocks or, rarely, animal dung, and the semiaquatic species may cement the eggs to water plants below the surface. Burrowing forms usually deposit theirs within the burrow, often in special chambers. In Ensifera the slender ovipositor is inserted into a substrate, usually the ground but wood or other plant tissue is frequently used; some species lay eggs singly on twigs, or on or in leaves; entrance is effected by alternate small penetrations of the valves, which slide longitudinally on each other. In Caelifera the pronged ovipositor penetrates by alternate opening and closing, drawing the abdomen after it; in the Acridoidea the latter may be stretched to twice its normal length in this way. Most Ensifera lay their eggs singly or in small groups, rarely loosely attached to one another by a very thin film. The Caelifera lay their eggs in batches of fewer than 10 to about 200, each batch being usually loosely held together by a proteinaceous foam, which at the same time often serves to cement the surrounding soil particles together to form a more or less discrete capsule, or 'pod'; several batches are commonly produced, at intervals of some days. Total egg production in the Orthoptera may reach many hundreds per female.

Facultative parthenogenesis is not uncommon, although fecundity is then usually much reduced and the viability of the progeny impaired. A very few species show obligate thelytoky, with males unknown or extremely rare.

Nymphs. After the intermediate moult, the nymph, in general, behaves in the same way as the adult. Sometimes, however, the 1st instar is more divergent, in both appearance and behaviour; thus in a few tettigoniids it may mimic an ant or a cicadeline beetle or even a seed or flower, but the resemblance diminishes in later instars and the adult is cryptic. Regeneration of damaged or lost legs is rare. The nymphal stage lasts some weeks or months.

Variation, Colour Adaptation. Intraspecific, genetic variation in conspicuous characters is widespread, especially in Caelifera, and includes polymorphism and continuous variation within populations, as well as geographical variation. Polymorphism may involve such structural features as wing and leg lengths, pronotal proportions, and surface sculpturing (see Dearn 1984). Strikingly different colour patterns may occur due to multiple alleles, or there may be polymorphism or continuous variation in colour of wing, hind tibia, etc. Geographical variation may involve similar features, along with percentage frequency of different morphs, and physiological characters such as diapause. Early instar nymphs may exhibit striking colour patterns which disappear in later instars.

Environmental factors may have a direct effect on the phenotype. Food quality affects overall size and general coloration, thus succulent vegetation causes increases in size and green coloration while in dry vegetation, size declines and brown coloration predominates (Farrow 1975). Under low temperatures individuals become darker through melanisation. Morphological colour adaptation to the background is widespread, especially among geophilous Acridoidea and in burnt vegetation, for example, black individuals may predominate. The males of *Kosciuscola tristis* show a reversible colour change under the control of temperature (Plate 2, J).

Phase Polymorphism. Phase polymorphism comprises a complex of responses to variations in population density (Uvarov 1966, 1977; Key 1954; Farrow 1974b) and is exhibited primarily in the Acridoidea, including six Australian species. It is best developed in locusts where increasing density results in the development of aggregative behaviour and the formation of hopper bands and swarms which migrate by day. At low densities, locusts remain isolated in the solitary phase, behaving as grasshoppers and migrating only at night. Transformations between solitary and gregarious phases are quite reversible between generations and intermediate forms in a transient phase also occur. Gregarious nymphs are distinguished from their solitary counterparts by their bright, aposematic coloration which serves to keep individuals aggregated in bands. Gregarious adults differ from their solitary counterparts by their brighter coloration and by their morphometrics, showing a higher elytron to femur ratio and a reduced sexual dimorphism. The principal function of gregarious behaviour is to prevent over-exploitation of food resources.

Phase differences are most marked in the migratory locust (*Locusta migratoria migratorioides*) (Farrow and Colless 1980). The differentiation is less in the yellow-winged locust (*Gastrimargus musicus*) (Common 1948), and plague grasshopper (*Austroicetes cruciata*) (Key 1954), and small in the Australian plague locust (*Chortoicetes terminifera*) (Key 1954) and wingless grasshopper (*Phaulacridium vittatum*) (Nicolas *et al.* 1982). Only colour differences are reported from *Austroicetes nullarborensis* (Key 1954). Morphological differences have not been reported in the spur-throated locust, *Nomadacris guttulosa* (formerly *Austracris*), in which the nymphs, unlike the adults, do not behave gregariously at high density (Farrow 1977b).

In Australia, outbreaks of the three main species of locust (Australian plague, spur-throated and migratory) result from drought-breaking rains in semi-arid grasslands (Baker and Casimir 1986). Concentration of solitary locusts in areas where rain has fallen, occurs as a result of migration at night during disturbed weather (D. P. Clark 1971). In the migratory and plague locusts, concentrated laying in egg-beds results in the production of gregarious populations. Emigration of swarming populations of plague and spur-throated locusts occurs at night during disturbed weather, ahead of frontal systems, and results in a displacement of infestations into agricultural areas of the south-east (Farrow 1977c). Once there, swarm movement by day results in a slow spread of infestations to the south-east; the infestations eventually die out as a result of movement into unfavourable environments. Outbreaks of grasshoppers, particularly of wingless grasshopper *Phaulacridium vittatum*, mixed with species of *Praxibulus* and *Austroicetes*, occur in improved pastures of south-eastern Australia during drought periods, accompanied by overgrazing (Farrow 1982d). Recently improved pastures in south-western Australia are also subject to chronic infestations of *Phaulacridium* spp.

Natural Enemies. In Australia, birds such as the straw-necked ibis are predators of locusts and grasshoppers. Nymphs and adults are preyed upon by a wide range of arthropods including sphecids, asilids, ants and spiders. Adults and sometimes nymphs are parasitised by Diptera, particularly the sarcophagid, *Blaesoxipha pachytyli*, and the nemestrinid, *Trichopsidea oestracea*, and more rarely, tachinids (Farrow 1982a). Ectoparasitic mites are common, especially species of the erythraeid genus *Leptus*. Many locusts and grasshoppers are susceptible to parasitisation by mermithid nematodes (Baker 1986) and by a fungus *Entomophaga grylli* (Milner 1978), particularly in wet conditions, while a protozoan, *Malamoeba locustae*, which commonly develops in laboratory cultures, is also recorded from the field (Ernst and Baker 1982). The egg pods of acridoids are attacked by parasitoids (*Scelio* spp.), which may migrate with their host (Farrow 1974a, 1981), by larvae of the melyrid beetle *Dicranolaius villosus* (Farrow 1974a), by larvae of the bombyliid, *Acridophagus flaviscutellaris*, and by mites.

Economic Significance. Locusts, grasshoppers and crickets are of major economic importance to crops and pastures in Australia. Plagues of the Australian plague

locust are frequent (every 2–3 years) and last 1–2 years, causing substantial crop and pasture losses in south-eastern Australia, particularly in dry years (Bullen 1975; Wright 1986a). Control operations and crop losses can amount to several million dollars in plague years. Plagues of spur-throated and migratory locusts are infrequent but protracted and cause high economic losses because they infest the summer cropping areas of eastern Australia (Baker and Casimir 1986). Severe plagues of wingless grasshopper (often accompanied by other grasshoppers in several genera) damage improved pastures in south-eastern and south-western Australia. Plagues occur in drought years when their economic impact has been greatest. Among the other families of Orthoptera only the field

cricket *Teleogryllus commodus* (Gryllidae) rates as a chronic pasture pest in cracking clay soils of western Vic.

Special Features of the Australian Fauna

The Australian orthopteran fauna reflects the world spectrum in number of species in the six larger superfamilies. Estimates show that the percentage of the world total occurring in Australia ranges to nearly 10 per cent except in the Gryllacridoidea where it reaches 15 per cent. There is a high percentage of endemism at the generic level—44% in the Grylloidea; 100% in the Tettigoniinae, about 90% in the Acridoidea. These figures are expected to be repeated in other groups when comprehensive revisions are undertaken.

CLASSIFICATION

Order ORTHOPTERA

(2827 Australian spp.)

Suborder ENSIFERA (1806)

GRYLLACRIDOIDEA (173)

1. Cooloolidae (3)
2. Stenopelmatidae (15)
3. Gryllacrididae (125)
4. Rhaphidophoridae (30)
- Schizodactylidae (0)

EUMASTACOIDEA (200)

9. Eumastacidae (200)
- Proscopiidae (0)

TRIGONOPTERYGOIDEA (0)

- Trigonopterygidae (0)

PNEUMOROIDEA (0)

- Pneumoridae (0)
- Xyronotidae (0)
- Tanaoceridae (0)

TETTIGONIOIDEA (900)

5. Tettigoniidae (900)
- Haglidae (0)

Suborder CAELIFERA (1021)

PAMPHAGOIDEA (24)

- Pamphagidae (0)
- Charilaidae (0)
- Lathiceridae (0)
- Ommexechidae (0)
10. Pyrgomorphidae (24)

ACRIDOIDEA (712)

- Lentulidae (0)
- Pauliniidae (0)

GRYLLOIDEA (733)

6. Gryllidae (715)
7. Myrmecophilidae (6)
8. Gryllotalpidae (12)

11. Acrididae (712)

TETRAGOIDEA (70)

12. Tetrigidae (70)

TRIDACTYLOIDEA (15)

13. Tridactylidae (9)
- Rhipipterygidae (0)
14. Cyldrachetidae (6)

There are many disparate classifications of orthopteroid insects (or portions thereof) at the present time. The overriding theme is the escalation of rank of categories above the tribal level. The lack of congruence among authors contributes to considerable instability. Readers should

consult Dirsh (1975) for the extreme of these views and Kevan (1982) for a synthesis of the classifications. Because of the general instability of higher classification in the group a conservative one, similar to that of the 1st edition is adopted here.

KEY TO THE SUBORDERS OF ORTHOPTERA

- Antenna with well over 30 segments (single exception, see Fig. 24.7 and text). [Auditory organs, when present, located on fore tibia; stridulatory specialisations of the fore wings, when present, located in the overlapping, horizontal part of the wings in their folded position; ovipositor, when present, having the valves articulated along their length to form an ensiform or stilettiform structure] ENSIFERA
- Antenna with less than 30 segments. [Auditory organs, when present, located on abdominal T1; stridulatory specialisations of the fore wings, when present, located in the lateral, subvertical part of the wings in their folded position; ovipositor, when present, consisting mainly of 4, separate, prong-like valves with a basal hinge articulation] CAELIFERA

Suborder ENSIFERA

Key to the Superfamilies, Families and Subfamilies of Ensifera Known in Australia

1. Tarsi 3-segmented GRYLLOIDEA.2
- Tarsi 4-segmented 11
- 2(1). Fore legs fossorial, with broad, flat femur and tibia, and with powerful teeth on both tibia and tarsus (Fig. 24.11B) Gryllotalpidae
- Fore legs normal, not especially modified (Figs 24.10, 11A) 3

- 3(2). Eyes greatly reduced (Fig. 24.11A); hind coxae closely approximated ventrally. [Small, depressed ant inquilines] **Myrmecophilidae**
 Eyes not reduced (Fig. 24.10); hind coxae well separated ventrally **Gryllidae.4**
- 4(3). Body generally covered with fine scales and flattened. Size small (usually less than 15 mm). ♀♀ apterous; ♂♂ with fore wings partly covered by pronotum (Fig. 24.10c) **MOGOPLISTINAE**
 Body not covered with scales, other characters not as above 5
- 5(4). Head prognathous. Tarsal claws bifurcate **OECANTHINAE**
 Head not prognathous. Tarsal claws not bifurcate 6
- 6(5). Hind tibia with teeth or spines between the dorsal spurs (Fig. 24.10G) 7
 Hind tibia without armature between dorsal spurs (Figs 24.10A, D–F) 8
- 7(6). Fore and mid tibia strongly banded; mid tarsal segment without prominent adhesive pads; head with bristles dorsally. ♀♀ apterous. [Long-legged species living in caves or on rock faces, or on tree trunks in rainforests] **PHALANGOPSINAE**
 Fore and mid tibia usually unbanded or with faint bands; mid tarsal segment with prominent adhesive pads; head usually without bristles dorsally. ♀♀ alate or apterous **ENEOPTERINAE**
- 8(6). Head with bristles dorsally (Figs 24.10D, F); hind tibia without teeth or spines anterior to dorsal spurs 9
 Head without bristles dorsally; hind tibia often with teeth or spines anterior to dorsal spurs 10
- 9(8). Hind tibia and femur nearly equal in length (Figs 24.10A, D); 2nd tarsal segment dorsoventrally flattened and bearing a prominent adhesive pad. Both sexes with fore wings. [Usually on vegetation] **TRIGONIDIINAE**
 Hind tibia distinctly shorter than hind femur (Fig. 24.10F); 2nd tarsal segment laterally compressed and without adhesive pad. One or both sexes with or without fore wings. [Ground dwelling, often in leaf litter] **NEMOBIINAE**
- 10(8). Fore tibia bearing inner and outer auditory tympana or only an outer tympanum, or no tympanum at all, but never having only an inner tympanum. ♂♂, when winged, with stridulatory file. [Field or ground crickets] **GRYLLINAE**
 Fore tibia bearing only an inner auditory tympanum. ♂♂ winged, without stridulatory file. [Small, plain, ground-inhabiting crickets] **PENTACENTRINAE**
- 11(1). Fore wings, when present, usually tough, ♂ tegmen usually with stridulatory apparatus; side of abdomen and adjacent inner face of hind femur without stridulatory modifications in either sex **TETTIGONIOIDEA-Tettigoniidae.12**
 Fore wings, when present, soft, pliable, without stridulatory apparatus; often side of abdomen and adjacent inner face of hind femur with pegs and modified spines as a stridulatory apparatus in both sexes and nymphs as well as adults **GRYLLACRIDOIDEA.24**
- 12(11). Head prognathous, body form phasmatoid (Figs 24.9C, F) 13
 Head not prognathous, body form not phasmatoid 14
- 13(12). Both sexes apterous, body form extremely slender (Fig. 24.9C) **PHASMODINAE**
 Both sexes winged or ♀ apterous, body form less slender (Fig. 24.9F) **ZAPROCHILINAE**
- 14(12). Head globose, not usually slanted or frontally flattened. Fore tibia in section approximately square in distal portion, dorsal surface not convex. Ovipositor usually short, upturned, laterally compressed. Prosternum unarmed **PHANEROPTERINAE**
 Without above combination of characters 15
- 15(14). Pronotum massive, posterior margin strongly acute; lateral margins crenulate or dentate. ♂♂ lacking modified stridulatory area of dorsum of tegmen **PHYLLOPHORINAE**
 Pronotum not as described above. ♂♂ with stridulatory region on dorsum of tegmen 16
- 16(15). Antennal sockets strongly rimmed, especially on internal dorsal margins. Thoracic auditory spiracle small, inconspicuous, not hidden by pronotum **PSEUDOPHYLLINAE**
 Antennal sockets not strongly rimmed. Thoracic auditory spiracle large, elongate, and, in most species, wholly or partially concealed by pronotum 17
- 17(16). Tibial auditory structure usually open; if closed on one side or both sides, then the slit is directed laterally and the opening is broad and its margins curving. Prosternum armed with a pair of spike-like processes **MECOPODINAE**
 Tibial auditory structure either open or closed, the slit distinctly directed dorsally in relation to position on tibia; if open, however, the opening is nearly uniform in width. Prosternum armed or unarmed 18
- 18(17). Prosternum unarmed; small, delicate, highly agile, arboreal and epiphyllid species, greenish or greenish yellow in coloration; tibial auditory structure generally open **MECONEMATINAE**
 Prosternum armed or unarmed; combination of other characters not as above 19
- 19(18). Prosternum unarmed; greenish, brachypterous species with the tegmina mostly concealed by pronotum; tibial auditory structure slit-like on both sides, appearing closed; size minute, 5–8 mm **MICROTETTIGONIINAE**
 Lacking above combination of characters 20
- 20(19). Fore tibia bearing a single apical spur on posterior margin of dorsal surface. Fastigium of vertex as broad as width of 1st antennal segment to half width of same. Hind basitarsus with a plantula which in most species is 1/2 the length of basitarsus **TETTIGONIINAE**
 Lacking at least 2 of the above-listed characters 21
- 21(20). Hind tibia lacking apical spurs on dorsal surface. Posterior portion of lateral lobe of pronotum produced or not produced **SAGINAE**
 Hind tibia with at least an external apical spur on dorsal surface, if not, then posterior portion of lateral lobe of pronotum produced 22

- 22(21). Frons vertical; mesosternum not spiniform. Sexually dimorphic (Figs 24.9B, D), ♂♂ winged, ♀♀ apterous TYMPANOPHORINAE
 Without above combination of characters 23
- 23(22). Fore tibia usually bearing 5–7 long, movable, outwardly bowed, opposing spines, the longest of which in many species is as long as or longer than the combined lengths of the first 2 tarsal segments. Fastigium of vertex narrow, strongly laterally compressed, its greatest width less than that of 1st antennal segment in most species and scarcely projected above same and usually sulcate LISTROSCELIDINAE
 Fore tibia of most species with spines not unusually lengthened and not as long as the combined lengths of the first 2 tarsal segments. Fastigium of vertex variable in width and not sulcate CONOCEPHALINAE
- 24(11). Tarsi depressed. [1st tarsal segment with plantulae; auditory tympana absent]..... **Gryllacrididae** 25
 Tarsi compressed
- 25(24). Antenna very short, reduced to 10 bead-like segments. Legs and body highly modified (Figs 24.7A, B). ♂♂ brachypterous, ♀♀ apterous **Cooloolidae**
 Antenna much longer, filamentous. Legs and body not abnormally modified (Fig. 24.8). Sexes not dimorphic for wings, but may be apterous or alate 26
- 26(25). 1st tarsal segment with plantulae; tibial auditory tympana present in all but one Australian genus **Stenopelmatidae**. 27
 1st tarsal segment without plantulae; tibial auditory tympana absent **Rhaphidophoridae**
- 27(26). Fastigium of vertex very narrow and distinctly sulcate, strongly compressed between antennal bases which nearly touch. Both sexes apterous DEINACRIDINAE
 Fastigium of vertex broader, not sulcate or compressed; antennal bases fairly widely separated. Fully winged, micropterous or apterous HENICINAE

Superfamily GRYLLACRIDOIDEA

The Gryllacridoidea is a primitive superfamily with nearly 1500 species world-wide. Superficially they resemble an insect intermediate in characters between katydids and crickets. The group includes 'king crickets' and 'camel' or 'cave crickets'. The following characters are additional to those given in the key. Antennae usually much longer than body (single known Australian exception, the Cooloolidae). Fore wings, when fully developed (Fig. 24.1A), pliable (single Australian exception *Anabropsis*), broad, often wrapping closely around each other and hind wings in repose, longitudinal veins running largely parallel, archdictyon absent; hind wings usually as broad as long. Costa often with several anterior accessory branches arising near its base in fore wing; Sc running parallel to C in both wings; R₁ usually with anterior branches, R_s with posterior; M often fused to R for part of its length, especially in hind wing; CuA in hind wing often fused at base with R+M. Abdomen with only central portion of sterna sclerotised (except in Cooloolidae and some Stenopelmatidae), S8 in female and S9 in male constituting subgenital plate; styles often present in male. Ovipositor present in all Australian species, ensiform with all 3 valves well developed (except in the Cooloolidae).

Most Australian species are pale to dark brown, nocturnal and spend the daytime hiding under bark or debris, or in burrows in the ground. Some are cavernicolous and some subterranean or partially so. Most gryllacridids and some stenopelmatids produce a silk-like substance from secretions of the mouth-parts; this substance is used to stabilise burrows or construct shelters of rolled leaves or detritus (Rentz and Weissman 1974; Morton and Rentz 1983). Phytophagous, granivorous and predacious or omnivorous feeding habits are represented. There is no comprehensive work on the Australian fauna and nearly two-thirds of the genera are endemic. [Karny 1937]

1. Cooloolidae. This peculiar, endemic family is repre-

sented by a single genus, *Cooloola*, from Qld. The family somewhat resembles the Stenopelmatidae (Figs 24.7A, B) but is recognised by a number of distinctive characters: general coloration pale; head round, moderate in size; antennae short, bead-like. Eyes small, almost vestigial in females of at least one species; maxillae with long, dagger-like laciniae which are uniquely longer in proportion to the mandibles and are used in digging. Hind femora very short; tibiae, especially fore tibiae, strongly modified for digging. Tegmina represented as abbreviated black pads in males and absent in females. All species are fossorial, females are probably permanently so, with males emerging at night during rainy periods to seek females. They appear to be predacious. The sperm of *C. propator* seem to be the most primitive known for any orthopteran (Baccetti 1987b). The karyotype of *C. ziljan* is 2n ♂ = 21(XO). [Rentz 1980, 1986, 1987b; John and Rentz 1987]

2. Stenopelmatidae. Mostly large, winged or wingless species with mandibles enlarged in some males. Fore coxa with a spine or tubercle. Fore tibia with auditory tympanum in all Australian species except *Onosandrus* from south-western W.A. Australian species have the dorsal surface of the fore tibia armed with one or more spines. Of six known genera, three are winged in both sexes, the others are apterous. All occur in the forests of the east coast except *Onosandrus*, which shares species with southern Africa. Of the four subfamilies, two occur in Australia. HENICINAE are represented by *Anabropsis* which also has representatives in the New World and south-east Asian tropics. *Australostoma* (Fig. 24.8A) is the sole representatives of the DEINACRIDINAE (king crickets). *Gryllotaurus* is unassigned to subfamily. The karyotype of only one species has been studied. In *Australostoma opacum* 2n ♂ = 22(XX). [Rentz and Weissman 1974; John and Rentz 1987]

3. Gryllacrididae (wood crickets, leaf-rolling crick-

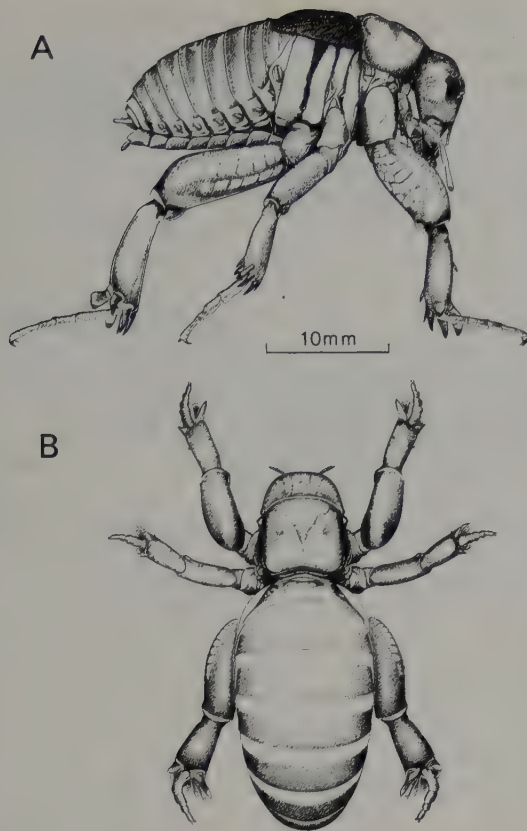


Fig. 24.7 *Cooloola propator*, Cooloolidae: A, ♂; B, ♀. [S. P. Kim]

ets). The largest family in the superfamily with 600 species world-wide. Most are fully winged (Fig. 24.8B) but some are apterous or brachypterous. Fore coxa usually well armed. Fore tibia armed dorsally only distally; tibial auditory tympana absent. Tarsi greatly depressed, 1st segment with plantulae. Late instars and adults of both

sexes are provided with a femoro-abdominal stridulatory apparatus which is used in time of stress. The mechanism may also be used in a sexual context but this has not yet been observed. Male distal abdominal segments in some species modified to form a 'scrotum' for testes. Ovipositor wide-ranging in shape and length. More than 20 genera have been recognised in the Australian fauna giving Australia a disproportionately rich fauna of these insects. Only *Bothriogryllacris* has been studied biologically. It has fully winged, burrowing species, which appear to be morphologically unmodified for their peculiar existence. They excavate burrows in the ground in arid Central Australia, line them with silk and provide the entrance with a cap of sand grains or a single stone, depending on the species. The cap is sewn tightly in place at dawn when the occupant returns from nocturnal foraging. Thus the cricket has a sealed chamber in which it avoids desiccation during the heat of the day. Food preferences for the family range from chiefly grass seeds in *Bothriogryllacris* to other arthropods in some *Hadrogryllacris* species. [Morton and Rentz 1983]

4. Rhaphidophoridae (camel crickets, cave crickets). Apterous, hump-backed cricket-like insects, usually with slender, elongate appendages (Fig. 24.8C). Fastigium of vertex narrow, and usually apically divided. Tarsi compressed, without plantulae. Tibial auditory tympana absent. All species are confined to wet forests, rock outcrops and caves. They are mainly omnivorous scavengers; one Australian species was observed to kill and feed upon newly hatched kestrel chicks (A. M. Richards 1970). Some are long-lived with one Australian species requiring 2.5 years to mature and going through 7 instars. Eight subfamilies have been recognised of which one, the MACROPATHINAE, has often been given familial status. Only Macropathinae occur in Australia; seven endemic genera have been described from the east coast, Tas. and the caves of the Nullarbor Plain. The subfamily has a circum-Antarctic distribution. [Ramsay 1979; A. M. Richards 1970, 1971b, 1987]

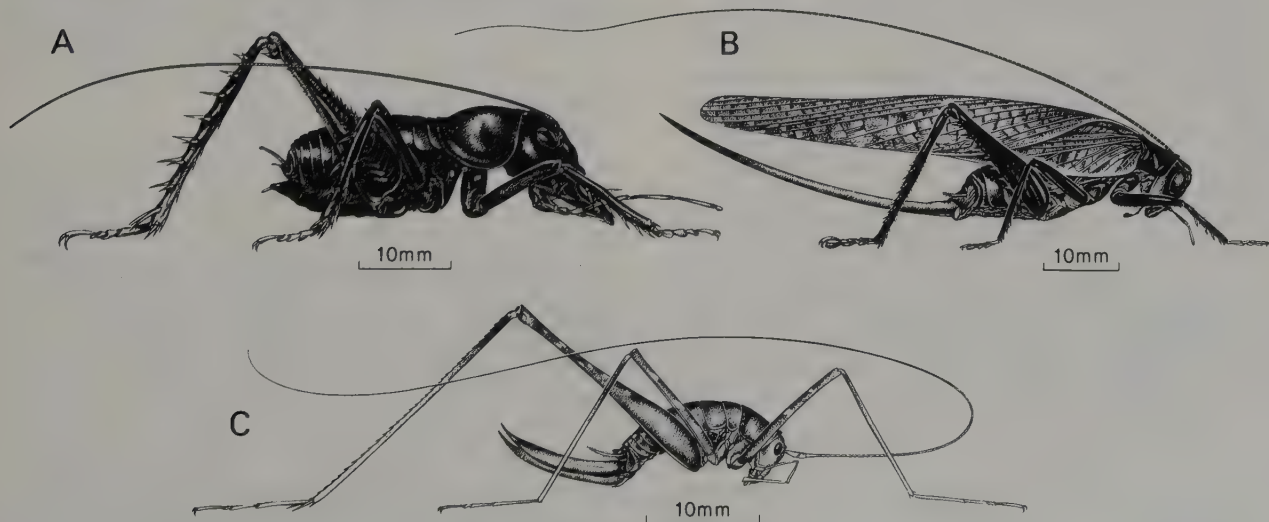


Fig. 24.8 A, *Australostoma opacum*, Stenopelmatidae, ♂; B, *Hadrogryllacris magnifica*, Gryllacrididae, ♀; C, *Macropathus tasmaniensis*, Rhaphidophoridae, ♀. [F. Nanninga]

Superfamily TETTIGONIOIDEA

The Tettigoniodea is the largest superfamily of the Ensifera with more than 5000 species. It is characterised by the following features additional to those given in the key. Antennae usually longer than body. Fore tibiae with auditory tympana except in the Australian subfamily Phasmodinae. Fore wing rarely absent in male; when present, usually the left fore wing overlaps the right. CuA with its most anterior branch (or the vein as a whole) fusing with MP for part of its length, in fore wing at least; CuP unbranched, running straight to the margin in hind wing. Male fore wing usually with cubital region specialised for stridulation; CuP, the vein principally affected, is bent towards the posterior margin of the wing before resuming its longitudinal course, the reflexed portion being thickened and toothed on the underside. Abdomen with S8 in female and S9 in male constituting subgenital plate; male cercus well sclerotised, not flexible; styles usually present in male. Ovipositor present, though sometimes small, laterally compressed, with all 3 pairs of valves well developed. Prothoracic spiracles and associated ends of tracheal system sometimes enlarged and modified for an auditory function. Legs, even if heavily spined, seldom modified for digging.

Katyids are widely distributed throughout the world, and though predominantly tropical many occur in temperate regions. Many are arboreal or bush dwelling. Some live in reeds and grasses and some on the ground. As a whole members of the group resemble plant foliage, bark, twigs, lichens and most commonly leaves, and they exhibit cryptic behaviour. Some immature stages mimic wasps, ants or spiders but as adults mimic leaves. Irritant substances are produced by some species and a few exhibit aposematic coloration. Most are nocturnal and some are active both day and night. Primitive katyids were probably predacious but predators are relatively few among the extant species. The majority eat foliage, flowers or seeds. Many are omnivorous or opportunistic scavengers.

A few katyids, at times, become strongly gregarious. Some flying species may swarm in the manner of locusts. Serious crop damage can occur under these conditions. The Tettigoniodea have been divided into numerous subgroups, and some subfamilies have been raised to family status relatively recently (see Kevan 1982). Here two families are recognised. The primitive Haglidae (= Prophalangopsidae) include only three living genera, none of which is Australian, and a number of fossils. [Rentz 1979, 1987a; Beier 1955; Kevan 1982]

5. Tettigoniidae (katyids, bushcrickets, long-horned grasshoppers). Tettigoniidae differ from Haglidae by having more advanced stridulatory specialisation. Fore wing folded along line between CuA and CuP, horizontal part relatively small in fully winged species, hind wing with first fold in MP area. Archedictyon usually present over entire fore wing and sometimes on a small distal portion of hind wing. MA almost always fused to Rs for short distance in hind wing and occasionally in fore wing; CuA with its most anterior branch (or the vein as a whole) usually fused with MP over whole of its distal portion.

The stridulatory mechanism of the fore wing has been described by Ragge (1955a).

Three subfamilies are endemic to Australia, the Microtettigoniinae, Phasmodinae and Zaprochilinae. The TYMPANOPHORINAE are known from the Malay Peninsula as well as both coasts of Australia; *Tympanophora* (Fig. 24.9B) is the only Australian genus (Riek 1976d). The TETTIGONIINAE include 17 genera and 72 species (Rentz 1985). Omnivorous and predacious habits are known and nocturnal, diurnal and crepuscular activity occurs according to the species. Except for the arid, central portion of the continent, tettigoniines inhabit most of Australia, including the tropics. Two unrelated genera are illustrated in Figs 24.9H, I. The PHASMODINAE are known from one genus with several species from W.A. They are apterous and phasmatoid (Fig. 24.9C). The fore tibia bears only a trace of the auditory tympanum. The hind tibia is of nearly uniform width throughout but the habit of the living katydid is clearly saltatorial. The ZAPROCHILINAE comprise three genera, one undescribed. *Zaprochilus australis* is a remarkable orthopteran (Fig. 24.9F) with a strongly prognathous head and narrow wings which rise at an angle from the body and are 'rolled' phasmatid-like. During the day, when the insect is inactive, it cryptically resembles a twig. *Anthophiloptera* is known from one large species, *A. dryas* occurring in mesic areas of coastal, eastern Australia. It has cryptic adaptations similar to those of *Z. australis* and lays its eggs in cracks in bark. Much smaller than *Zaprochilus* is an undescribed genus in which males are micropterous and females apterous. Phasmodines and zaprochilines are primarily floral feeders. The former feed on all parts of the flowers of a wide range of native and introduced plants and often damage the flowers on which they feed. Zaprochilines, on the other hand, seem to feed only on the pollen and nectar of their hosts and do not obviously damage the flower. Most of the phasmodine and zaprochiline species are adult in late winter and spring.

The MICROTETTIGONIINAE are known from one genus with species in coastal S.A. and W.A. They are small, about 5–7 mm, micropterous, diurnal predators of small insects. The subfamilies PSEUDOPHYLLINAE, MECOPODINAE and PHYLLOPHORINAE are represented by a few genera mainly confined to the tropics.

The CONOCEPHALINAE are well represented with over 20 genera in 4 tribes. Rentz and Gurney (1985) placed the colourful species of *Metholce* and *Veria* together with a related genus from Chile in the Coniungopterini. Conocephalini are best represented by *Conocephalus* (Fig. 24.9G) with more than 30 species, many of which were included in the work of Pitkin (1980). The tribe is well represented in northern tropical and eastern Australia and is absent from the south-west. Most are associated with grasses. Agraeciini are best represented in the tropics and are characterised by a spiny appearance and a spini-form fastigium of the vertex. They are primarily floral and fruit eaters. Copiphorini or cone-headed katyids are associated with grasses and reeds where they feed on seeds. Males chorus, often loudly, at twilight or in the afternoon on overcast days and their monotonous, loud,

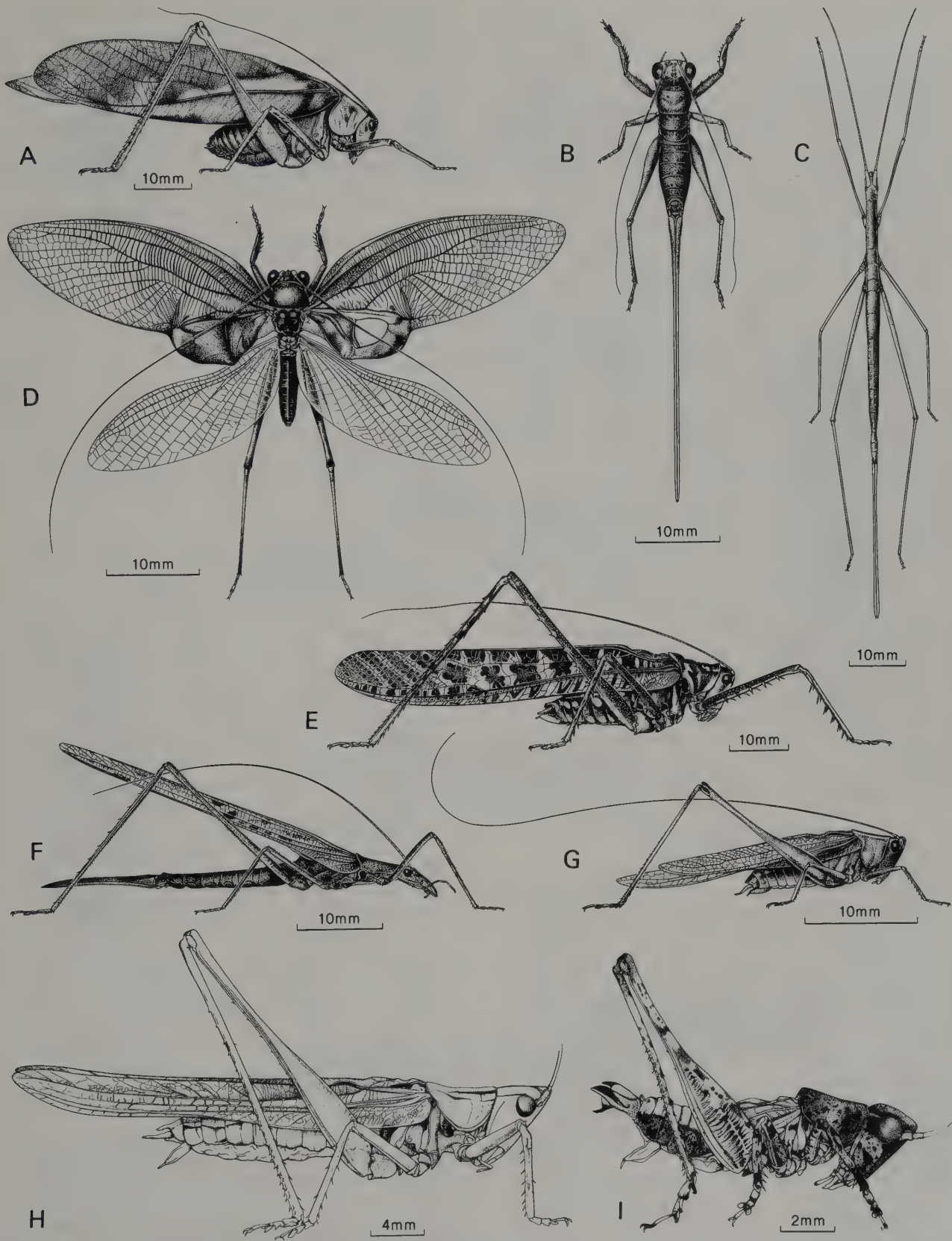


Fig. 24.9 Tettigoniidae: A, *Caedicia major*, Phaneropterinae, ♀; B, *Tympanophora pellucida*, Tympanophorinae, ♀; C, *Phasmodes ranatriformis*, Phasmodinae, ♀; D, *T. pellucida*, ♂; E, *Chlorobalius leucoviridis*, Listroscelidinae, ♂; F, *Zaprochilus australis*, Zaprochilinae, ♀; G, *Conocephalus upoluensis*, Conocephalinae, ♂; H, *Metaballus alatus*, Tettigoniinae, ♂; I, *Ixalodectes megacercus*, Tettigoniinae, ♂.

[A–G by F. Nanninga; H–I by C. Mullinex Tibbetts]

buzzing calls are familiar to visitors to grasslands and coastal habitats in northern Australia. Bailey (1979) reviewed the Australian species. The LISTROSCOLIDINAE are represented in Australia by a range of disparate genera all of which have a low, rounded profile to the fore tibia which lacks dorsal spines and bears very elongate, ventral spines. The elongate, conical head of the group is indicative of their predatory nature. *Chlorobalius leucoviridis* (formerly *Yorkiella picta*) (Fig. 24.9E) is a beautiful, mottled green and white representative which is broadly distributed throughout arid Australia. The Australian SAGINAE are similar in some respects to the Listroscolidinae but are generally more robust, and have round heads. They are found on or around flowers where they feed on floral parts and occasionally insects. The MECONEMATINAE are small, delicate katydids of temperate and tropical forests. Australian examples are micropterous in the male and apterous in the female. They are small and greenish and the 1st and 2nd tarsal segments are laterally grooved. Their habits have not been studied. The PHANEROPTERINAE, the largest subfamily of the Tettigoniidae, are characterised by a relatively small number of genera but some have large numbers of species. *Caedicia* is probably the largest Australian genus of orthopteroid insects. Its species are more or less very similar in appearance (Fig. 24.9A). *Alectoria superba* (Plate 2, K) is the most spectacular species of the group and bears an enormous pronotal crest. The mountain katydid, *Acripeza reticulata*, is a widespread, familiar species in eastern Australia particularly in the southern Alps. It is almost black and sexually dimorphic. Males are elongate and fully winged; females (Plate 2, L) are very robust and bear shell-like tegmina. When either sex is disturbed, the tegmina are raised to reveal brightly coloured red and blue bands on the abdomen. The neck membrane is bright orange. In addition, the disturbed insect reflex bleeds. All of this serves an aposematic function.

Superfamily GRYLLOIDEA

The Grylloidea, or true crickets (including tree crickets and mole crickets), comprise nearly 3000 species in more than 350 genera. Fore tibiae bear auditory tympana on one surface or the other in most species that stridulate. Non-stridulating species often lack auditory tympana. All tarsi 3-segmented. Fore wings, when fully developed, relatively broad, usually tegminised, folded near their mid-line, in region of median vein, to form box-like cover for meso- and metathorax and the proximal part of hind wings and abdomen; horizontal part relatively much longer than in Tettigonioidae, in male most of it modified for stridulation in almost identical fashion in the two tegmina; right tegmen usually overlaps left. Hind wing folding to form attenuate spike usually projecting well beyond fore wing. Many species brachypterous or apterous, or polymorphic for wing length. Costa usually absent or reduced in tegmen; Sc lying well behind anterior margin in tegmen, with numerous parallel, sinuous, anterior accessory branches; in hind wing Sc running just behind C; R, M and CuA closely approximated to Sc along the mid-line of fore wing, with M usually branching in its

distal part; CuA in male fore wing giving rise to posterior accessory branches which contribute to stridulatory apparatus, in hind wing dividing at base with parallel branches which run straight to wing margin; CuP in male tegmen bending strongly towards posterior margin before continuing towards apex, with stridulatory teeth on ventral surface of bent section (Fig. 24.1B); 3 anals in tegmen, which in male fuse with each other and CuP and then separate again, and in female run separate and parallel to margin; anals numerous in hind wing. Abdominal sterna fully sclerotised, S8 in female and S9 in male constituting subgenital plate which lacks styles. Cerci similar in both sexes and usually long and flexible. Ovipositor, when present, usually stilettiform, composed of 2 pairs of valves, the 3rd being greatly reduced.

The Australian crickets were monographed by Otte and Alexander (1983) who recognised 492 species in 85 genera. They hypothesised that on the basis of the similarity of the two faunas most Australian crickets reached the continent from New Guinea by way of Torres Strait. The vast majority of cricket species occur in the north-eastern portion of the continent, the fewest in the south-west. The rainforest species show strong relationships with those of New Guinea.

Most crickets are omnivorous and are not host specific. Certain species tend to be found at characteristic levels above the ground rather than on a particular type of vegetation. Others seek the topmost branches of whatever tree they are in. Some favour saplings or low grass. Dozens of species live on or near the ground in burrows or cracks. Some species are gregarious. Nearly all Australian habitats are occupied by one or more cricket species. *Eucalyptus* and *Acacia* harbour few crickets.

Tropical crickets show pronounced adult seasonality. Even in northern Qld rainforest species are highly seasonal. Crickets in the north, including grasslands, seem to have longer adult lifespans, perhaps even extending beyond one season. This would seem to be an adaptation to cope with the irregular weather patterns in that area. Crickets sometimes cause economic concern, especially during drought years when numbers of certain species such as *Teleogryllus commodus* build up and feed on already sparse, pasture grasses. The grylline *Yarrita pikiara* has been reported in large numbers in Vic. where it damages pasture grasses from time to time.

Gorochov (references in Desutter 1987) provided a new, radical classification of crickets which elevated many subfamilies to family status. Desutter (1987) provided a similar study based solely on male genitalia and compared his results with those of Gorochov. The classification followed here is basically that of the 1st edition of this text. With the exception of the Gryllotalpidae and Myrmecophilidae, which are given family status, the classification is the same as that of Otte and Alexander (1983). There are good arguments for raising some subfamilies, including the Eneopterinae, Mogoplistinae and Oecanthinae to family status (see Kevan 1982 or Vickery 1977). The Cachoplistinae, although originally recorded from Australia and India, probably do not occur in Australia (see Otte and Alexander (1983) for discussion).

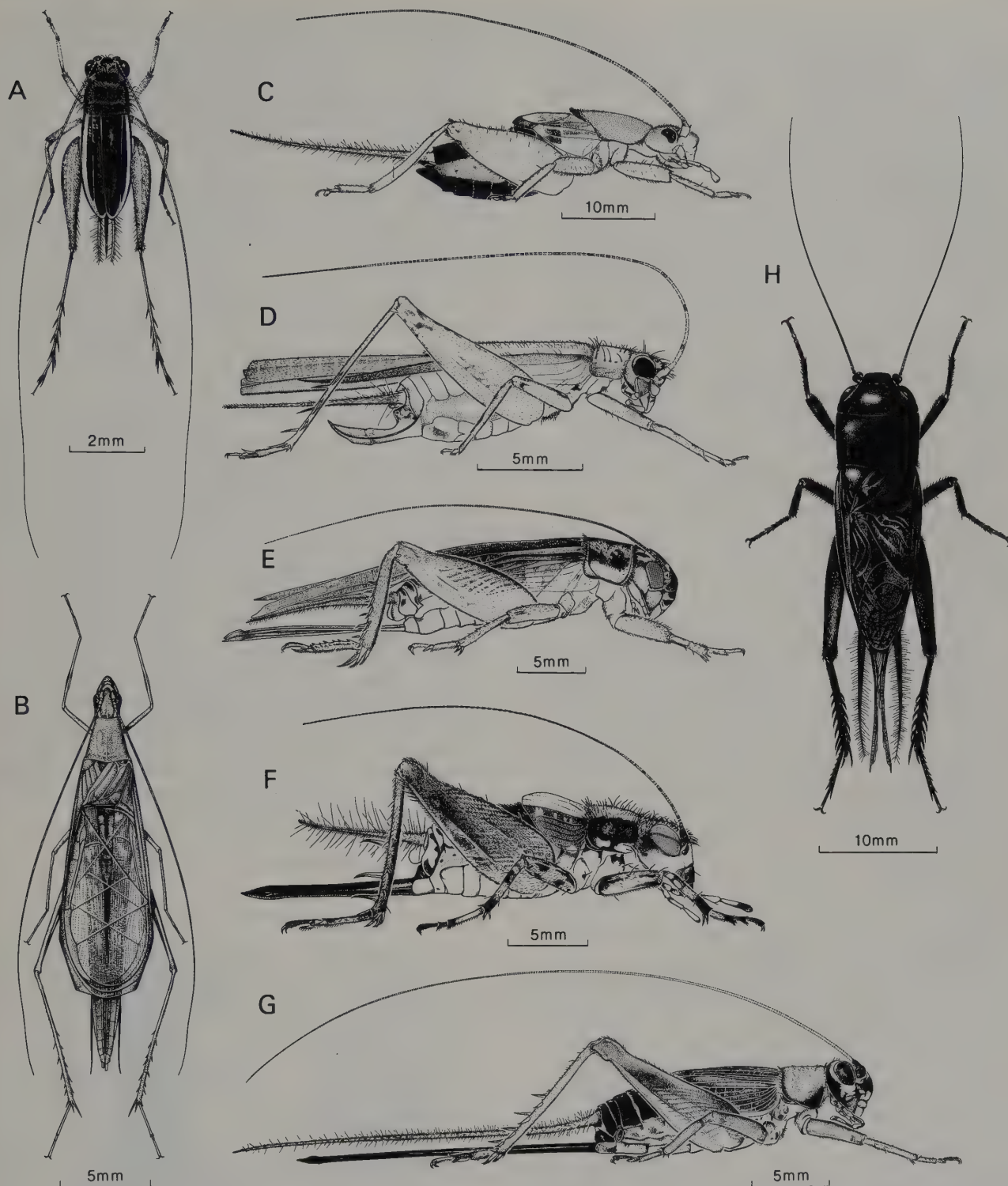


Fig. 24.10 Gryllidae: A, *Balamara albobittata*, Trigonidiinae, ♀; B, *Oecanthus rufescens*, Oecanthinae, ♂; C, *Talia pitonga*, Mogoplistinae, ♂; D, *Amusurgus kanyakis*, Trigonidiinae, ♀; E, *Lepidogryllus comparatus*, Gryllinae, ♀; F, *Bobilla neobivittata*, Nemobiinae, ♀; G, *Myara aperta*, Eneopterinae, ♀; H, *Teleogryllus commodus*, Gryllinae, ♂. [A, B, H by F. Nanninga; C–G by S. Smith]

6. Gryllidae. This is the largest family of crickets. Some species are apterous and subterranean but by far the largest number are winged in both sexes. The stridulatory apparatus of the male tegmen (Fig. 24.1B) usually includes four areas: the mirror, cordal area, harp and basal

areas. Three posterior branches of CuA delimit the mirror and form the boundary between the cordal area and harp, while the proximal boundary of the last is formed by CuP. The GRYLLINAE include 6 tribes based on tegminal structure, vein patterns and tibial spination formulae.

Gymnogryllini include a single genus of very large, forest-dwelling crickets from northern Australia. Cephalogryllini include 3 genera, of which *Apterogryllus* is wingless and subterranean. Gryllini include the widespread *Teleogryllus* and the introduced house cricket *Acheta domesticus*. Landrevini include only 2 Australian genera, both from the rainforests of North Qld. *Mjobergella* has a large, square head; *Copholandrevus* is peculiar in that the short male tegmina do not bear a stridulatory file. Gryllomorphini are a large tribe with 10 genera world-wide but only 2 in Australia. Both occur in the dry interior. *Eurygryllodes* includes 16 ground-dwelling species in which the males are winged and which occur in the arid deserts. In *Malua* both sexes are wingless. There are 13 Australian genera of Modicogryllini, including some of our most common crickets. *Loxoblemmus* has a flattened, leaf-like face. *Lepidogryllus* contains 2 common, widespread, sympatric species which can only be satisfactorily determined by song. Not included in the above tribes is the introduced domestic pest *Gryllodes supplicans* (= *sigillatus*) which is common in Perth and north-western Australia as well as in the Brisbane and Sydney areas. The NEMOBIINAE are very small, ground-dwelling crickets; 7 genera are known from Australia. *Pteronemobius* is the only genus with species capable of flight. It is distinctive in having the proximal internal spine of the hind tibia short and knob-like. *Bobilla* contains many species principally from the south-east corner of the continent. The TRIGONIDIINAE occur widely throughout Australia but are best represented in the tropics. Eleven genera are known from Australia, some of which are world-wide in distribution. Most species have a stridulatory file. The PENTACENTRINAE are represented by *Pentacentrus* which also occurs in South-East Asia and the Pacific; species generally resemble nemobiines, have flat heads and have no stridulatory mechanism. PHALANGOPSINAE (3 genera, 32 spp.) are slender, long-legged crickets found on rocks, tree trunks and logs, and in cave entrances. In *Endotaria* both sexes are wingless, in *Tathra* and *Endacusta* only females; males are loud stridulators.

ENEOPTERINAE (105 spp.) include 3 widespread tribes: Eneopterini (10 genera, usually in drier regions), Pseudoscirtini (9 genera) and Itarini (2 genera, 2 spp.; in Qld rainforests).

The monotonous song of OECANTHINAE (tree crickets; 2 genera, 7 spp.) is a typical, nocturnal sound in the arid, grassland habitats of inland Australia. MOGOPLISTINAE (scale-bearing crickets; 11 genera, 80 spp.) are small and occur in arid as well as rainforest habitats on leaf surfaces, in grasses, in tangles of dead stems or in tree tops. They are highly ventriloquial and a singing male may move or change position during intervals of chirps.

7. Myrmecophilidae. The 'ant crickets' are small, apterous, flattened crickets which live as inquilines in ant nests. Two genera are recognised with about 42 species. The world-wide distribution of *Myrmecophilus* suggests an ancient origin for the family. Eyes reduced; all coxae large and closely approximated ventrally; cerci with pseudosegmentation; ovipositor short, stout, strongly and

rigidly descending, supported at base by long descending processes of T8 and T9. These crickets resemble Trigonidiinae, some of which occur in leaf litter, and ant crickets may have diverged from the ancestors of that subfamily. Ant crickets feed on secretions of the ants but no one has discovered how they move from nest to nest. They lay incredibly large eggs for the size of the female, each egg being about 1/3 her size. Some species are parthenogenetic. A linear dominance hierarchy in which size and age play a primary role has been described in an American species of *Myrmecophilus* (Henderson and Akre 1986).

8. Gryllotalpidae (mole crickets). The family includes 5 genera with about 50 species world-wide. Australia is well represented with 10 species in *Gryllotalpa*. Lord Howe I. harbours an endemic genus *Triamescaptor*. Most species are large and winged and are often attracted to lights. The pronotum has the lateral lobes bending around ventrally, but not approximated on the mid-ventral line as in the superficially similar Cydrachetidae. Species with glabrous pronota are generally found in sand, those with strong pubescence are found in 'light soils'. The hind legs are relatively small, but the femur is considerably larger than the mid femur. Tegmen of male with harp and basal area, delimited as in Gryllidae, but with no differentiation of mirror and cordal area, only the most proximal branch of CuA being reflexed; ovipositor absent. Mole crickets make deep, permanent burrows as well as foraging galleries. Eggs may be brooded in elaborate chambers. Both sexes stridulate. The horn-shaped entrance chamber of the burrow is used differently by different species to increase the male's acoustical output (Nickerson *et al.* 1979). Although most species are thought to be herbivorous with some causing crop and turf damage, some are carnivorous on soil insects. [T. J. Walker 1984]

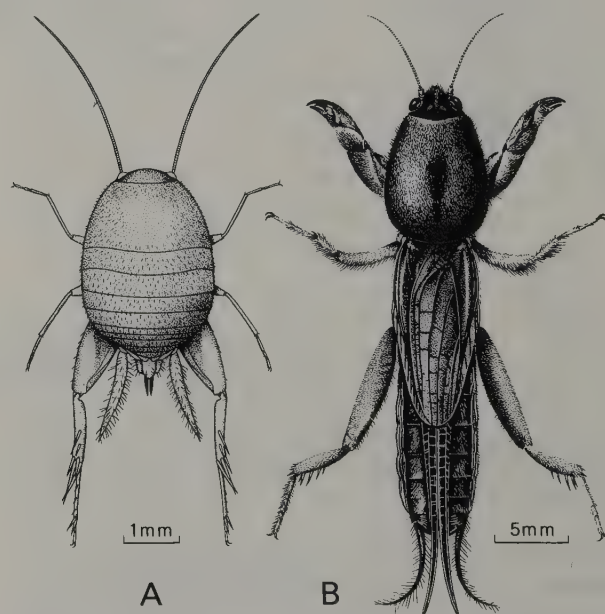


Fig. 24.11 A, *Myrmecophilus testaceus*, Myrmecophilidae, ♀; B, *Gryllotalpa* sp., Gryllotalpidae, ♀.
[F. Nanninga]

Suborder CAELIFERA

Key to the Superfamilies, Families and Subfamilies of Caelifera Known in Australia

1. Tarsi of all legs 3-segmented 2
- Tarsi of fore and mid legs at most 2-segmented 8
- 2(1). Head with posterior margin more or less emarginate dorsally, exposing the (often sclerotised) cervical membrane (Figs 24.12A, B); hind tibia with the two ventral, apical spurs much reduced or absent EUMASTACOIDEA-Eumastacidae. 3
- Head with posterior margin entire, not exposing cervical membrane (e.g. Figs 24.14A-C); hind tibia with all four apical spurs well developed 4
- 3(2). Both sexes wingless; head with basioccipital slit and with dorsal cervical sclerites; body very elongate, often stem or straw-like (Figs 24.12B, C; Plate 2, I); head usually long and pointed and with a long rostrum. Legs usually not held strongly akimbo (Fig. 24.12B) at rest MORABINAE
- One or both sex(es) usually winged; head without basioccipital slit and not bearing dorsal cervical sclerites; body subcylindrical and not elongate or stem-like; head not pointed, with a short, low frontal rostrum. Legs held strongly akimbo (Fig. 24.12A) at rest BIROELLINAE
- 4(2). Fastigium of vertex with a mediolongitudinal sulcus extending backwards for a short distance from its anterior extremity PAMPHAGOIDEA-Pyrgomorphidae
- Fastigium of vertex without a mediolongitudinal sulcus anteriorly ACRIDOIDEA-Acrididae. 5
- 5(4). Prosternum armed with a tubercle or collar 6
- Prosternum unarmed, if bearing a collar then antennae strongly ensiform ACRIDINAE
- 6(5). Genicular lobe of hind femur (knee) with a spine-like apex OXYINAE
- Genicular lobe of hind femur unarmed 7
- 7(6). Mesosternal lobes rectangular CYRTACANTHACRIDINAE
- Mesosternal lobes rounded or obtuse CATANTOPINAE
- 8(1). Pronotum produced posteriorly, overlying the remainder of thorax and the first few abdominal segments (Fig. 24.16B); hind tarsus 3-segmented TETRIGOIDEA-Tetrigidae. 9
- Pronotum nearly covering at most rest of thorax; hind tarsus 1-segmented TRIDACTYLOIDEA. 12
- [The tetrigoid subfamilies are poorly defined and the key below should be used with some caution.]
- 9(8). Facial shield broadly developed below ocelli; pronotum strongly compressed, often arcuate, crested CLADONOTINAE
- Facial shield narrowly developed below ocelli; pronotum not normally arcuate or elevated, if so, then not crested ... 10
- 10(9). Lateral lobe of pronotum with posterior angles produced, flexed or slightly bent upwards SCELIMENINAE
- Lateral lobes of pronotum with posterior angles not produced, if so, then not strongly bent upwards 11
- 11(10). Lateral lobes of pronotum with posterior angles acute, prominent METRODORINAE
- Lateral lobes of pronotum with posterior angles rounded TETRIGINAE
- 12(8). Body form as in Fig. 24.16A; hind legs saltatorial Tridactylidae. 13
- Body form as in Fig. 24.16C; hind legs not saltatorial Cyllindrachetidae
- 13(12). Tarsus of hind tibia without subapical spine TRIDACTYLINAE
- Tarsus of hind tibia with subapical spine DENTRIDACTYLINAE

Superfamily EUMASTACOIDEA

This superfamily has been reclassified recently in different ways. The Proscopiidae, thought to be related to the Australian endemic eumastacid subfamily Morabinae by Blackith (1973), has been placed in a superfamily on its own (see Kevan 1982). In the latter work 11 families were ascribed to the Eumastacoidea. Here only one family is recognised, the Eumastacidae which includes two subfamilies in Australia, the Morabinae and the tropical Biroellinae. The superfamily contains some 1000 species in 240 genera. Figs 24.11A-C illustrate diverse examples. The majority live in the tropics but a number of groups, such as the Morabinae, are found in mild temperate regions. Most species live on trees and shrubs; some live on grasses; many resemble parts of plants. Eggs are probably laid in the ground, but it is hard to imagine some tree-dwelling species doing so. They are usually laid in small groups and they are not bound together in an egg case.

This superfamily is distinguished by the relatively short, non-tubular prothorax, which is seldom more than

twice as long as wide. The average size tends to be small with the body seldom exceeding 45 mm. The head usually lacks basioccipital slits (exception, the Morabinae) and the neck normally lacks dorsal cervical sclerites. The antennae are usually very short. The fore and mid legs are not unusually slender and the hind metatarsi are serrulate or spined or have a dorsal tubercle. The ovipositor valves are slender and strongly denticulate suggesting an ovipositional site in plant tissue rather than in the ground. Many species are nocturnal.

9. Eumastacidae (monkey grasshoppers). This family is considered in the broad sense (not Kevan 1982) and includes two Australian subfamilies. The following additional characters may be noted. Antenna with one or more of the distal segments bearing a small tubercle on ventral surface; hind legs with femur, at rest, rotated so that its outer surface faces substrate with the tibia flexed against it. Fore wing (when fully developed) with CuA unbranched; hind wing with M unbranched, CuA reduced, and an ambient vein around the anal area. Abdominal spiracles located in pleural membrane.

Auditory tympanum absent. Male genitalia (see Dirsh 1961; Key 1976) very diverse. Hind gut with 6 caeca in some groups (see Grant and Rentz 1967). The MORABINAE are represented in Australia by some 40 genera containing over 250 species in several tribes. Key's (1976, 1977) generic classification was based primarily on genitalia. All known species are apterous. They are mostly found on trees and bushes but many species are found in association with grasses. Some appear host specific, others are associated with distinct kinds of habitat. Chromosome numbers range from $2n \text{ ♂} = 13\text{--}21$ and include two large metacentric pairs, the AB and CD chromosomes, or their transformation products resulting from dissociations, fusions, inversions or translocations. Blackith and Blackith (1967, 1969b) studied the anatomy and physiology of the Morabinae and discussed variation (1969c) in anatomical characters and have made observations on various other biological topics (1969a). Blackith and Blackith (1969a) reared *Perilitus morabinarum* (Braconidae), the first hymenopteran recorded as a primary parasite of any grasshopper or locust. A tachinid, *Myothyria fergusonii*, is a common parasite of morabines and certain acridoids. White and Contreras (1979, 1981) reported on the cytogenetics of the parthenogenetic *Warramaba virgo* and its bisexual relatives and its probable origins. Mesa and Ferreira (1981) used chromosomes to hypothesise that the South American Proscopiidae and Australian Morabinae have had a common ancestor. The works by M. J. D. White (1977, 1979, 1981, 1982) on population genetics in tandem with the taxonomic studies of Key (1977, 1979, 1981a, b, 1982) are classics in speciation literature. The BIROELLINAE consist of a single described genus (Fig. 24.11A) with about 30 species mostly from New Guinea but with good representation in tropical Australia. The subfamily has been elevated to a

family (Gomphomastacidae) by some authors. It is recognised, in addition to the characters given in the key, by having the antennae short and filiform and with 11–14 segments. The hind tibiae have only one inner and one outer apical, articulated spur; the 2nd inner spur is reduced; the 2nd outer spur is vestigial or lacking. The hind metatarsi are virtually unarmed, or slightly tuberculate dorsally. The male cerci characteristically have long, narrow, upwardly directed apical teeth. No comprehensive taxonomic work has been done on the subfamily but M. J. D. White (1975) studied the karyotypes of one species from Cape York Peninsula and two from New Guinea. The Cape York species has $2n \text{ ♂} = 17$ karyotype which resembles those of many morabine species whereas the New Guinea examples had little in common with any morabine.

Superfamily PAMPHAGOIDEA

This superfamily includes only one Australian family, the Pyrgomorphidae, of the 5 included by Dirsh (1975). This is the largest family of the group. Species of Pamphagoidea range from small-sized grasshoppers to some of the largest grasshoppers known. They are characterised by having (1) the lower basal lobe of the hind femur mostly longer than the upper or both of them nearly the same length and (2) a fastigial sulcus. Gonopore processes which are a pair of ventral processes from the basal valves of the penis are absent.

10. Pyrgomorphidae. All Australian Pyrgomorphidae have conical heads and an elevated median process is present on the prosternum of all known species. The fastigium often has the region near the margins raised and uneven and separated from the central portion by lateral sulci which join the median sulcus anteriorly to form a Y. The integument varies from smooth to granular, rugose or

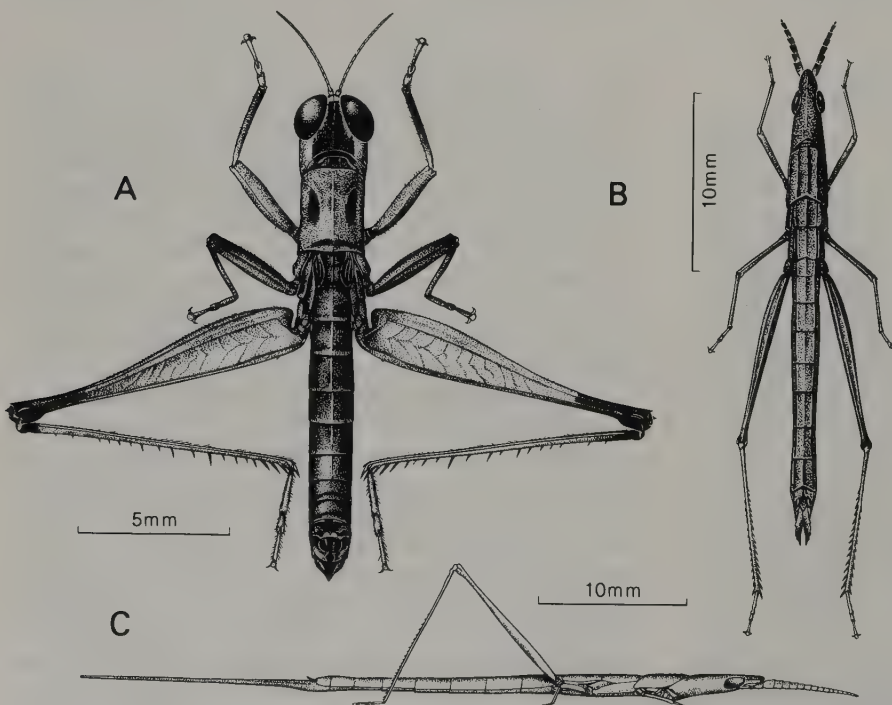


Fig. 24.12 Eumastacidae: A, *Biroella* sp., Biroellinae, ♂; B, *Keyacris scurra*, Morabinae, ♀; C, *Warramunga desertorum*, Morabinae, ♂. [F. Nanninga]

tuberculate. Only two subfamilies are recognised with only one, the PYRGOMORPHINAE, occurring in Australia. This subfamily has been divided into 31 tribes, 5 of which occur in Australia. The Psednuriini, revised by Key (1972), is an endemic tribe with three slender (Fig. 24.13C), stem-like genera found around the coastal margins of the continent. They are found on upright, monocotyledonous plants where they reside head upwards. The Atractomorphiini comprise only an African genus and *Atractomorpha* (Fig. 24.13A) which has a widespread distribution in Africa, Asia and Oceania and 3 species in Australia (Key and Kevan 1980). The population cytogenetics of *Atractomorpha similis* in Australia has been studied by John and King (1983). The Desmopterini (Fig. 24.13B) contribute two genera which live in leaf litter or on bushes and trees in the northern rainforest. The most spectacular tribes are the endemic Petasidini and Monistriini (Key 1985). The beautiful Petasidini (*Petasida*, *Scutillya*) are the most spectacular Australian grasshoppers. Petasidini and Monistriini are usually associated with plants belonging to a restricted group of families that are aromatic. These hosts seem to contribute a distasteful quality to the grasshoppers which is reflected by their aposematic coloration (e.g. Plate 2, H). Petasidini are fully winged. The 4 genera of Monistriini comprise species that are wholly brachypterous or in which a percentage of specimens are fully winged. In both tribes males frequently ride on the backs of the much larger females even when not in copula. The basic chromosome number of both tribes is $2n \text{ ♂} = 19$. Peters (1981) has worked extensively on the cytogenetics of the species.

Superfamily ACRIDOIDEA (grasshoppers, locusts)

The Acridoidea is the largest superfamily of Orthoptera. More than 8000 species in 1500 genera are known world-wide. Grasshoppers are usually moderate in size but there are many Australian species under 10 mm in length. Locusts are species which occasionally form dense, migratory swarms. These are often encountered in inland Australia; world-wide about 20 species from several subfamilies of Acrididae form migratory locust swarms.

General characters of the Acridoidea in addition to those given in the key are: antennae not excessively long, not longer than body, not moniliform and lacking definite antennal organs. Tarsi with arolium; basal segments of hind tarsi lacking dorsal spines and tubercles. Wings variable, from fully developed to apterous. Fore wing (tegmen), when fully developed, with the more proximal parts of Sc, R and M (but not Cu) closely approximated (Fig. 24.1C). Hind wing with only anal area folding in repose; R and M fused, at least towards the base. Both wings with CuP tending to reduction. Abdominal sterna fully sclerotised, lacking separate laterosternites; 8 sternites visible in female, 9 in male, the last of which is the subgenital plate. Cerci short, often species specific in shape in males, unsegmented. Paraprocts without articulated cerciform processes. Gonopore processes present or absent. Dirsh (1956) reviewed the male genitalia of the

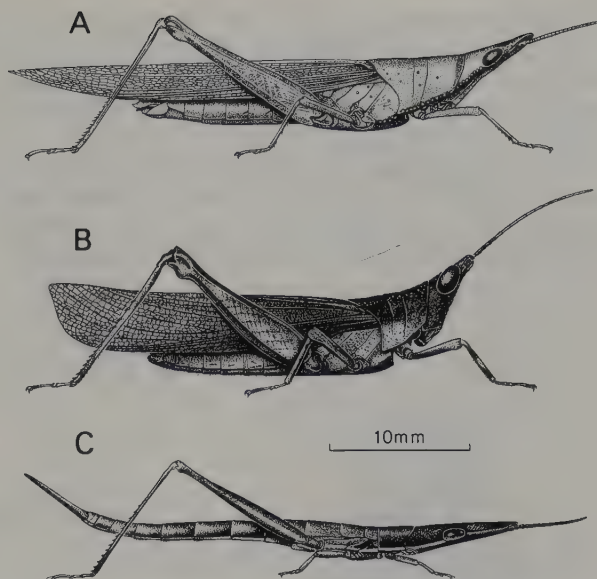


Fig. 24.13 Pyrgomorphidae: A, *Atractomorpha similis*, ♀; B, *Desmoptera truncatipennis*, ♀; C, *Psednura pedestris*, ♂. [F. Nanninga]

superfamily. Usually they are well sclerotised, consisting of an epiphallus and intromittent phallus (aedeagus) which is often species distinctive. Ovipositor always present. Various kinds of stridulatory apparatus are present, usually best developed in the males. Some grasshoppers stridulate by rubbing the mandibles together.

Most grasshoppers are diurnal but much activity such as feeding, mating, moulting and flying takes place at night. Grasshoppers are exclusively phytophagous ranging from species that feed on grasses to those with specific host requirements. A small number feed on dead leaves and lichens.

Uvarov (1966, 1977) gives a comprehensive account on the biology, biogeography, behaviour and population dynamics of grasshoppers. Sjöstedt (1921, 1936) and Rehn (1952–57) began a series of monographs on the Australian species, and Key (1986) published a synonymic checklist recognising 736 species in 218 genera. The general biology of Australian species was reviewed by Key (1958, 1959).

The Acridoidea are largely xerophilous and only a few species penetrate further than the margins of rainforests in Australia. The predominant element in the superfamily is ancient and autochthonous (Key, 1959). Dirsh (1961) recognised 14 families in the Acridoidea including 3 from Australia but in the present chapter all Australian acridoids are incorporated in one family, the Acrididae. The band-winged grasshoppers, often placed in the Oedipodinae (= Locustinae), and including such genera as *Gastrimargus* and *Sphingonotus* are here included in the Acridinae.

11. Acrididae. This is the largest family of Caelifera. The species exhibit little of the specialisation seen in the other acridoid groups. Dirsh (1961) recognised 17 subfamilies, including 6 from Australia; only 4 of the latter are currently recognised. No representatives of the sound-

producing Gomphocerinae, which are common in the Northern Hemisphere, occur in Australia. At the generic level there is 90% endemism. The most common chromosome number throughout the world is $2n \delta = 23$ but numbers as low as 8 are known.

Chromosomal studies have been made of *Austroicetes interioris* (Nankivell 1967), *Goniaea australasiae* (Peacock 1970) and a gynandromorph *Valanga irregularis* (M. J. D. White 1968). For the *Caledia captiva* com-

plex Shaw and Wilkinson (1980) have studied chromosomal differentiation and the population genetics of a hybrid zone, and Daly *et al.* (1980) the distribution of chromosomal and allozymic variation in relation to reproductive isolation.

The OXYINAE include 12 genera of Indo-Malayan origin. Many are associated with water and grasslands. *Oxya japonica*, one of the most destructive grasshoppers in rice fields in South-East Asia, also occurs in Australia where

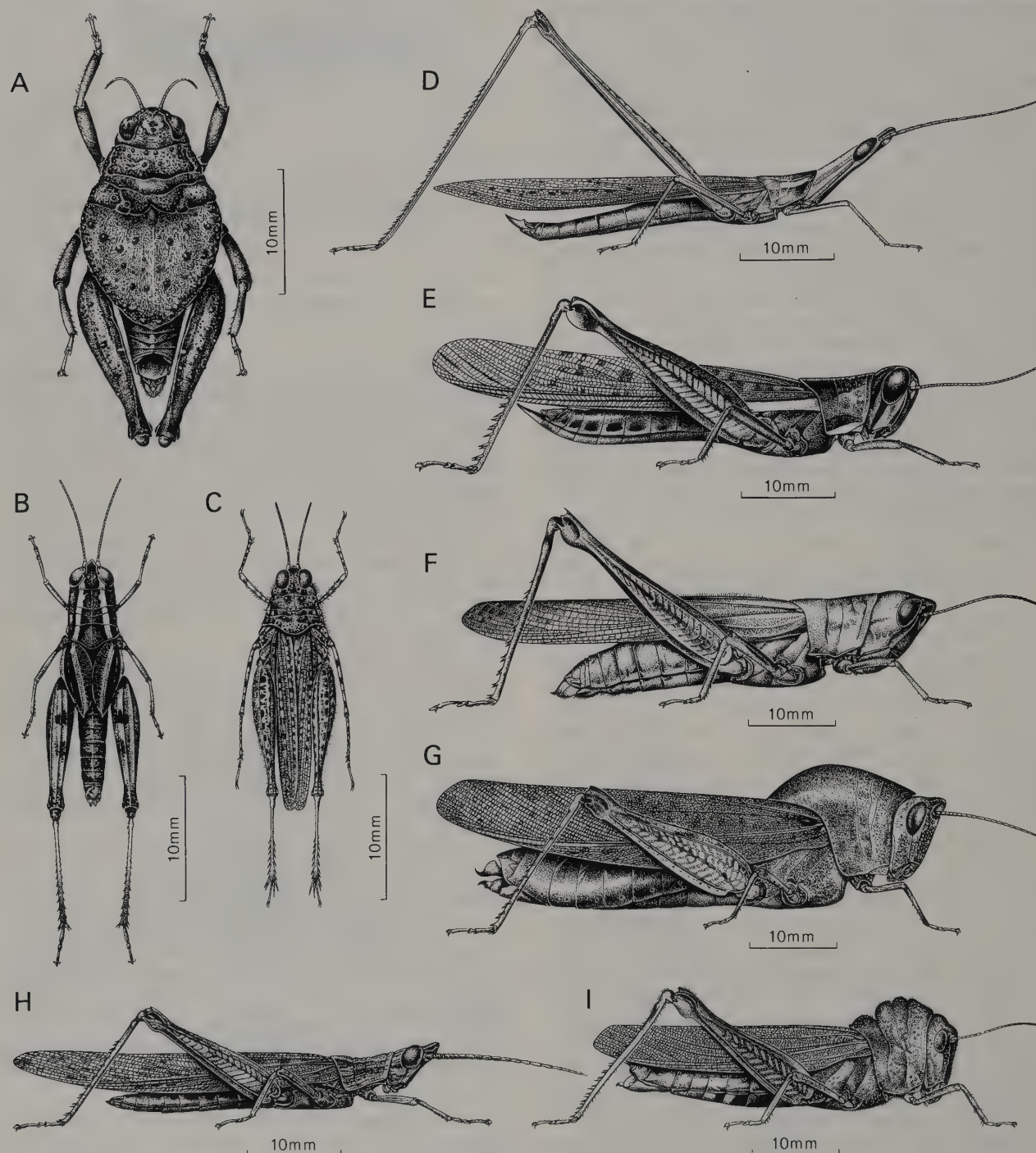


Fig. 24.14 Acrididae: A, *Raniliella* sp., Catantopinae, δ ; B, *Phaulacridium vittatum*, Catantopinae, δ ; C, *Ursiella rubropunctata*, Catantopinae, δ ; D, *Acrida conica*, Acridinae, δ ; E, *Nomadacris guttulosa*, Cyrtacanthacridinae, δ ; F, *Bermiella acuta*, Oxyinae, δ ; G, *Goniaea australasiae*, Catantopinae, δ ; H, *Coryphistes ruficola*, Catantopinae, δ ; I, *Ecphantus quadrilobus*, Catantopinae, δ .

[F. Nanninga]

it does minimal damage. *Bermiella acuta* (Fig. 24.14F), which occurs on sedges, rushes and grasses near water, has a number of adaptations for semiaquatic life, such as dense patches of hairs on the distal abdominal sterna and tegmina and an air chamber formed by the doming of the costal area of the tegmen over the 1st abdominal spiracle. John and Freeman (1976) have studied the chromosome systems of 3 species of the tropical and subtropical oxyine *Tolgadia*.

The spur-throated grasshoppers of the CATANTOPINAE comprise 84% of the Australian acridoid fauna. This is a disparate percentage when compared with other regions of the world. *Goniaea* (Fig. 24.14G) is a typical example with species living among fallen leaves under eucalypts. Their cryptic coloration and the leaf-like shape of nymphs render them invisible until they move. *Coryphistes* (Fig. 24.14H) is found on tree trunks, dead branches and leaf litter where it is also cryptically concealed. *Ecphantus quadrilobus* (Fig. 24.14I) is velvety green or light brown and seems restricted to plants of the genus *Sida*. Of all the grasshoppers only one genus, *Phaulacridium*, is shared with New Zealand. *P. vittatum*, the wingless grasshopper (Fig. 14.14B), is predominantly brachypterous but macropters become more numerous as population densities increase (Nicolas *et al.* 1982). It is of economic importance because of the damage it does to pastures (see D. P. Clark 1962; Farrow 1982d). Dearn (1984 for refs.) has studied colour pattern polymorphism in this species as it relates to habitat and distribution, as well as the influence of inheritance and natural selection in maintaining pattern polymorphism. *Raniliella* (Fig. 24.14A) has an enlarged pronotum with dorsal tubercles which help to conceal it on stony substrates. *Urnsiella rubropunctata* (Fig. 24.14C) has very long mid legs which it uses to bury itself in sand at dusk.

The large spur-throated grasshoppers of the CYRTACANTHACRIDINAE are represented by large, mostly tropical species. Some of the world's most important locust pests are in this subfamily. Both Australian genera, *Nomadacris* and *Valanga*, have Malayan and Pacific distributions. *Nomadacris guttulosa* (formerly *Austracris*), the spur-throated locust (Fig. 24.14E), is found all over Australia although it is primarily adapted to tropical grasslands in which the adults overwinter in reproductive diapause often roosting in trees and shrubs. Maturation and oviposition at the onset of the rains of summer has been studied by Farrow (1977a). Plagues originate from these grasslands and may damage both dicotyledonous and monocotyledonous summer crops (Elder *et al.* 1979; Casimir and Edge 1979). One of the world's largest acridoids is *Valanga irregularis*, a species of the tropics and subtropics, which feeds on leaves of trees and shrubs and can cause some damage to fruit and nut trees.

The ACRIDINAE is a large group with world-wide distribution. Several locusts are included. This group contains some of the most phylogenetically advanced grasshoppers with 22 genera and 33 species known from Australia. About one-third of this total is contributed by Old World genera. For example, *Acrida* (Fig. 24.14D), *Gastrimargus* (Plate 2, F) and *Sphingonotus*, are represented in

Australia by single species. *Chortoicetes terminifera* (Fig. 24.15) is the most important Australian locust pest; it is characterised by a black spot at the tip of the hind wing (see Key 1958; Casimir 1962). Other important contributions concerning this species are as follows: on the frequencies and inheritance of pattern morphs (Byrne 1967); on the protein and amino acid content of the haemolymph in relation to diet and hydration (Djakusumah and Miles 1966; Muljadi 1967), on egg development in relation to temperature and moisture, with reference to the induction of diapause (Wardhaugh 1972; Gregg 1983; Hunter and Gregg 1984); on flight, the factors initiating it, and its significance in migration (D. P. Clark 1969, 1971; Drake and Farrow 1983; Hunter *et al.* 1981); on plague dynamics and field ecology (L. R. Clark 1947; D. P. Clark 1972; D. P. Clark *et al.* 1969; Farrow 1977a,b,c; Farrow and Longstaff 1986; Key 1954; Symmons and Wright 1981; Wright and Symmons 1987); and, finally, on population dynamics (D. P. Clark 1974, 1978; Farrow 1979, 1982a, 1982b). One of the most important Old World locust pests, *Locusta migratoria migratorioides*, is widely distributed in coastal and sub-coastal grasslands but only one plague has broken out to date; this occurred between 1973 and 1976 (Elder *et al.* 1979). The Australian population is identical to the tropical race of this locust (Farrow and Colless 1980). Sound production by males is well developed in this family and varies from stridulation by the hind femora in *Schizobothrus flavovittatus*, to wing clicking in *Gastrimargus musicus* and *L. m. migratorioides*, and the wing buzzing produced by *Froggattina australis* (Plate 2, G) in flight. [Ritchie 1982; Vickery 1977]

Superfamily TETRIGOIDEA

The Tetrigoidea include some 1000 species of small, greyish grasshoppers, sometimes called 'grouse-locusts' or 'pygmy grasshoppers'. They are characterised by the following distinctive features. Frons below median ocellus bearing median carina, which divides ventrally, forming, with fronto-clypeal suture, a 'supra-clypeal triangle'. Pronotum usually reaching or surpassing apex of abdomen, shielding wings (if present), sometimes modified in bizarre fashion. Prosternum expanded along its anterior edge to form collar around mouth-parts and directly connected to pronotum by precoxal bridge. Fore and mid tarsi 2-segmented, hind tarsus 3-segmented; arolia absent. Hind legs saltatorial. Fore wing reduced to small, usually oval, lateral scale, which is sharply divided by strong radial vein into exposed, sclerotised, morphologically anterior region, and membranous, posterior region covered by lateral edge of pronotum; all other veins greatly reduced or absent. Hind wing with all veins unbranched, except for basal division of Cu; remigium reduced to narrow band, with marginal C; M fused with R for all or nearly all its length, and for much of its length closely pressed against Sc; CuA very short; anal fan large, 1A closely pressed against CuP for almost all its length. Both wings often absent, or concealed and functionless. Abdomen with discrete laterosternites; female subgenital plate constituted by S8, that of male by lobe of

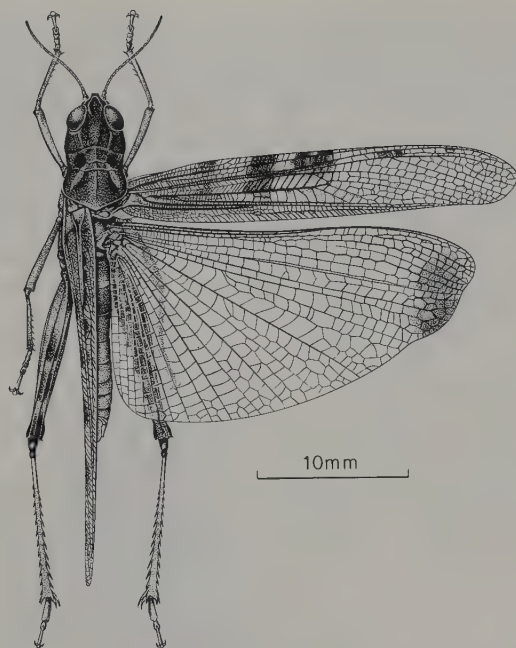


Fig. 24.15 *Chortoicetes terminifera*, Acrididae-Acridinae, ♂. [F. Nanninga]

S9; without styles. Females of at least some species (*Tetrix* spp.) bear a complex spermatophore chamber which receives the inordinately large spermatophore during copulation. Spermatheca relatively small and trilobed (Farrow 1963). Cerci short, unsegmented. Paraprocts without cerciform processes. Male genitalia simpler and quite differently constructed from those of the Acridoidea. Ovipositor as in Acridoidea. Auditory and stridulatory organs absent. Abdominal spiracles located in pleural membrane. So far as known, all Tetrigoidea have a karyotype with $2n \text{ ♂} = 13$, all chromosomes being acrocentric.

Complicated pattern polymorphism is characteristic of many Tetrigoidea, as well as polymorphism in pronotal length, with which differences in rugosity and other structural features are correlated. Some flightless species are neotenic in pronotal development. The insects are found exposed on bare soil or sand, less often on short turf, and usually in damp situations. Many species swim freely, and may remain for some time under water, resting on the bottom or clinging to water plants. Tetrigoidea feed principally on algae and other cryptogams, or on mud, from which they presumably obtain living or dead vegetable matter. In the species studied, the eggs are laid in small batches in the soil, without any bonding secretion. They are cylindrical, with a slender appendage at the anterior pole.

12. Tetrigidae. This family has been divided into 9 or 10 often poorly delimited 'sections', which are sometimes treated as subfamilies; Rehn (1952) recognises 4 in Australia. About half of the genera are endemic. *Paratettix* (Fig. 24.16B), with several Australian species, has a wide extra-Australian distribution. Key (1981b) designated lectotypes for the Australian species. A rain-forest species *Vingselina brunneri* has been observed to

ascend tree trunks to about 2 m from the forest floor after dark.

Superfamily TRIDACTYLOIDEA

This superfamily comprises only a few genera and some 146 species. Its components were formerly classified under the Grylloidea, species of *Tridactylus* being sometimes called 'pygmy mole crickets'. The true relationships of the group (Ander 1934) have been shown to lie with the Tetrigoidea. There is, however, a remarkable parallelism between the Tridactyloidea and the Grylloidea, the Tridactylidae corresponding to the Gryllidae, and the Cyllindrachetidae to the Gryllotalpidae. The following features are common to the constituent families. Prosternum directly connected to pronotum by precoxal bridge. Fore tibia in all Australian species strongly fossorial: expanded and equipped with powerful teeth (*dactyls*). Fore tarsus 1- or 2-segmented, inserted on inner face of tibia (cf. Gryllotalpidae); mid tarsus 2-segmented; hind 1-segmented; arolia absent. Abdomen with 9 fully sclerotised sterna in both sexes, S9 constituting subgenital plate, which lacks both styles and sternal lobe. Günther (1969) noted the presence of repugnatorial glands on the abdomen. Paraproct bearing sclerotised hook in male. Ovipositor absent in all Australian species. Three families are recognised. One, the Rhipipterygidae, is Neotropical. Günther (1978) revised the Australian fauna.

13. Tridactylidae. Tridactylids are very small, usually smooth and shiny, black or variegated. Eyes well developed. Pronotum overlapping mesonotum, its lateral lobes well separated by broad prosternum. Fore femur little expanded, tibia moderately so, tarsus 2-segmented. Messner (1969) described a glandular opening on the mid tibia of *Tridactylus*. Hind legs saltatorial, with greatly enlarged femur; tibia long and slender, with 4 terminal spurs long, especially ventral pair, and several more distal spines along dorsal edges often replaced by articulated lamellae; tarsus sometimes greatly reduced. Fore wing tegminised, falling well short of abdominal apex (even when hind wing much surpasses abdomen), bearing 2 veins (probably Sc and R) and sometimes a third (probably 1A). Hind wing, when fully developed, with remigium reduced to narrow sclerotised band, all veins unbranched, except Cu; C weak, supporting proximal part of anterior margin; R, M and CuA fused or closely associated in basal third of wing; anal fan large, with very numerous anals, traversed by single arc of cross-veins. Putative stridulatory mechanism (Figs 24.5E, F) sometimes located ventrally on fore wing, along distal part of Sc. Cercus 2-segmented in all Australian species. Paraproct bearing cerciform appendage. Karyotypes with $2n \text{ ♂} = 13$ (XO) and 15 (XO) have been reported (John and Rentz 1987).

These little insects usually frequent the margins of water bodies, where they construct galleries in sandy ground. However, they spend much of their time crawling about on the surface and are active day and night. The hind legs are kept flexed during walking; they are used only for making extremely powerful jumps when disturbed, and for swimming on and beneath the surface of

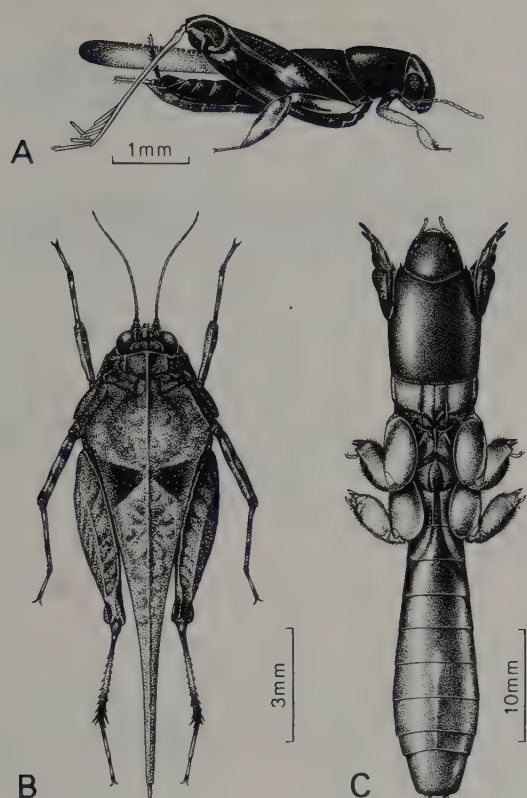


Fig. 24.16 A, *Tridactylus australicus*, Tridactylidae, ♂; B, *Paratettix argillaceus*, Tettigidae, ♀; C, *Cyindracheta psammophila*, Cyindrachetidae, ♀.
[F. Nanninga]

the water, when the tibial lamellae presumably come into action. Both subfamilies occur in Australia. The TRIDACTYLINAE include the cosmopolitan genus *Tridactylus* (Fig. 24.16A; 2 widespread spp.) and *Xya* (5 spp.) (one of

which has been segregated into subspecies). *Dentridactylus* (DENTRIDACTYLINAE) occurs in Australia (2 spp.) and Brazil (1 sp.).

14. Cyindrachetidae. This is a family of medium-sized, cylindrical, larviform, wholly subterranean insects comprising six described species; six species occur in Australia, one in New Guinea, and one in Patagonia. Eyes reduced, ocelliform. Mandibles and maxillary palps (Figs 24.5A–D) modified for stridulation. Pronotum not overlapping mesonotum, its lateral lobes curving around ventrally and approximated on the mid-ventral line (cf. Gryllotalpidae, p. 386). Fore femur and tibia greatly flattened and expanded, the latter with very large teeth (dactyls); the tarsus 1- or 2-segmented, slender, without dactyls (cf. Gryllotalpidae). Hind legs not saltatorial; femur scarcely larger than mid femur; tibia short and stout, with stout terminal spurs and no dorsal spines or lamellae. Wings absent. T9 and T10 partly fused; supranal plate flexed into a position ventral to T10. Cerci stout, unsegmented, ventral in position, often directed forward. Paraproct without cerciform appendage. There are two genera, *Cyindracheta* (sandgropers; Fig. 24.16C) in Australia and New Guinea, and *Cyindroryctes* in Patagonia. The first is unique in Orthoptera in possessing a thin, tubular, strongly projecting mesothoracic collar, which envelops the hind part of the pronotum, while allowing it free movement in all directions. The insects are found tunnelling in sand in both humid and arid regions. *C. psammophila* sometimes damages wheat in W.A. Two species have been studied cytologically (John and Rentz 1987). In *C. psammophila* $2n\delta = 15$ (XO) and in *Cyindroryctes spagazzinii* the $2n\delta = 13$ (XO).

ACKNOWLEDGMENTS. The author wishes to thank Drs R. A. Farrow, T. Yamasaki, D. R. Ragge and Mr J. Balderson for helpful comments.

Phasmatodea

(Stick-insects)

K. H. L. KEY

Mandibulate, phytophagous, exopterygote Neoptera, having all legs gressorial, with small, well separated coxae; pronotum without large descending lateral lobes; wing rudiments of nymph not reversing their orientation in the later instars; specialised auditory organs lacking; eggs free, thick-shelled, provided with a conspicuous operculum.

The Phasmatodea are large to very large terrestrial insects, inhabiting chiefly the warmer parts of the world, especially the tropics. They have attracted wide attention because of their size—a few species exceeding 30 cm in length—and the remarkable resemblance of most of them to sticks or leaves. The wingless, parthenogenetic *Carausius morosus* is a widely studied laboratory animal. The stick-insects were long treated as a family within the Orthoptera. They are now given ordinal rank, but under a variety of names: Cheleutoptera, Phasmida, Phasmodea, Phasmatodea, Phasmoptera, Phasmatoptera. The works of Beier (1957, 1968), although in some respects outdated, remain the most comprehensive accounts of the order. A recent book, *Stick Insects: Phylogeny and Reproduction* (see Scali and Mazzini 1987) contains a number of important papers on subjects covered by the title and some others. Basic structure and habits are rather uniform. More than 2500 species are known.

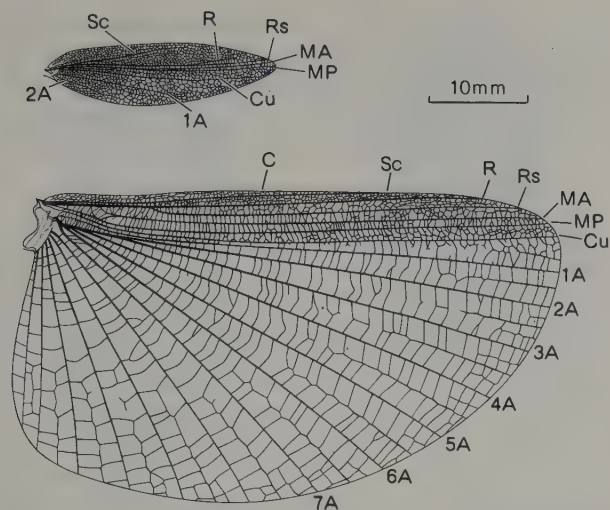
Anatomy of Adult

Males of most species are markedly smaller and more slender than the females and may differ from them in many striking structural features.

Head. Typically prognathous, rectangular to oval, sometimes horned or spined. Antennae short to very long and slender, with 8 to more than 100 segments. Eyes rather small, situated anterolaterally. Ocelli present only

in some winged species, then normally 3, larger in the male or confined to that sex. Mouth-parts comprising strong, cutting mandibles; maxillae with 5-segmented palp, 2-segmented galea, and a toothed lacinia bearing bristles on its inner face; and labium with 3-segmented palp, well developed paraglossae, and smaller glossae. Hypopharynx present.

Thorax. Prothorax shorter than the other segments, transverse to little more than twice as long as broad, movable on the mesothorax; pronotum transversely arched, without strongly descending lateral lobes, usually with a transverse and a median sulcus; prosternum sclerotised, comprising large, well separated basisternum and sternellum of about equal size; propleura well developed, the episternum and epimeron subequal. Mesothorax reaching well forward from the level of attachment of the fore wings, longer than the other segments, ranging from only slightly so to very elongate, often spiny or granulose; mesonotum transversely arched. Metathorax rigidly connected to the mesothorax, often elongate in apterous species. Meso- and metathoracic sterna comprising a large basisternum, with a much smaller bilobed sternellum and a small spinasternum; pleura strongly oblique to longitudinal, with long and sometimes slender episternum and smaller, sometimes very small, epimeron, those of the metathorax extending posteriorly well beyond the extremity of the notum and often reaching that of T1. Spiracles

Fig. 25.1 *Podacanthus wilkinsoni*, wings of ♂.

[F. Nanninga]

situated anterior to the meso- and metathoracic episterna.

Legs. All 3 pairs gressorial, usually long and slender, often spined, occasionally bearing lobes or broad expansions. Coxae rather small, usually well separated. Fore femora usually curved and compressed proximally to accommodate the head when the legs are extended forwards in the mid-line. Tarsi of all Australian species 5-segmented (except in regenerated legs, where they are nearly always 4-segmented), with terminal claws and arolium. In some groups the mid and hind tibiae have a more or less evident triangular area, the 'area apicalis', delimited ventrad at their apices.

Wings. Most Australian species are apterous in both sexes. When wings are present, they are usually fully developed and functional in the male (Fig. 25.1), but frequently reduced in the female. Fore wings tough opaque tegmina, nearly always short and covering only the base of the hind wings at rest, overlapping each other across the mid-line, usually with a knob-like dorsal eversion in the proximal half, which accommodates a prominence of the hind wing-base in the folded position; occasionally reduced to spines or absent, even when the hind wings are present. Hind wings broad, remigium tough and opaque like the fore wing, the large anal area membranous, in repose folded fanwise and overlain by the protective remigium. Venation (Ragge 1955b) very uniform, with restricted branching; C absent in fore wing, in the hind wing marginal, unbranched, and usually weak; Sc unbranched; R usually unbranched in the fore wing, but in the hind usually breaking into R_1 and R_s , either of which may occasionally be itself bifurcate; M usually bifurcate in the fore wing, in the hind bifurcate in the basal part of the wing, or occasionally trifurcate; Cu unbranched; anals unbranched, usually one in the fore wing and many in the hind, of which the relatively weak first arises separately, with the second to seventh in one group and the rest in another.

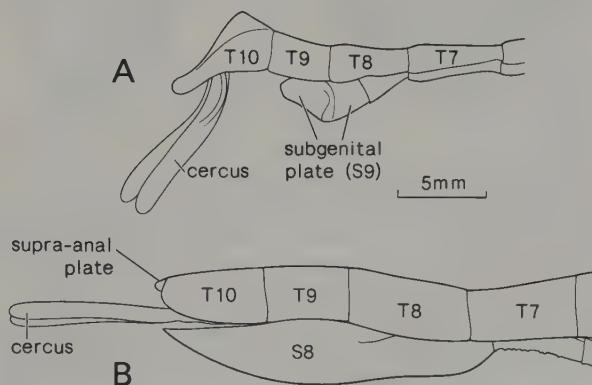
Abdomen. Cylindrical or dorsoventrally compressed, sometimes bearing spines or lobular outgrowths, consist-

ing of 11 segments. T1 (often termed the 'median segment') rigidly connected to the metanotum in all Australian species, the intervening suture sometimes lost; T10 well developed, in the male often emarginate posteriorly and with the ventroposterior angles produced and sometimes caliper-like, their inner extremities usually provided with small teeth or spines, the lateral walls of the tergum sometimes curving round ventrally, or even meeting on the mid-ventral line anteriorly; T11 constituting the supra-anal plate, which is often concealed beneath T10, especially in the male, but in the female may be elongate and either articulated on T10 or fused to it. S1 reduced and usually not identifiable; S10 usually well developed, fused posteriorly to the paraprocts, which represent the divided S11. Cerci unsegmented, long or concealed beneath T10, occasionally modified as claspers in the male. Spiracles situated in the pleural membrane near the ventroanterior angle of T2–T8 and in a small sclerite below T1.

In the male (Fig. 25.2A), S9 constitutes the subgenital plate; it lacks styles, but bears a somewhat swollen, cup-shaped, distal lobe, sometimes called the 'poculum'. S10 is provided in some groups with a backwardly directed, sclerotised, usually prong-shaped copulatory process, the *vomer* (Fig. 25.3). Genitalia (Snodgrass 1937) concealed by the subgenital plate, comprising an asymmetrical group of largely membranous lobes.

In the female (Fig. 25.2B), S8 is the subgenital plate; it consists of a scoop- or keel-shaped structure known as the 'operculum', whose free posterior end may project beyond the abdomen. The ovipositor, enveloped below by the operculum, consists of 3 pairs of slender valves.

Internal Anatomy. Alimentary canal straight, with a large crop, of which the posterior portion functions as a gizzard; mid gut long, in its anterior part provided with circular folds and in its narrower posterior part with numerous external glandular papillae, each bearing a terminal filament; caeca absent or rudimentary. Salivary glands large, bilobed. Numerous Malpighian tubules, arranged in 2 groups, open into the intestine by a common duct. The central nervous system includes 3 thoracic and 7 discrete abdominal ganglia. The male reproductive system comprises a pair of narrow, elongate testes, with a tubular seminal vesicle opening into each vas deferens

Fig. 25.2 *Podacanthus wilkinsoni*, apex of abdomen in lateral view: A, ♂; B, ♀.

[F. Nanninga]

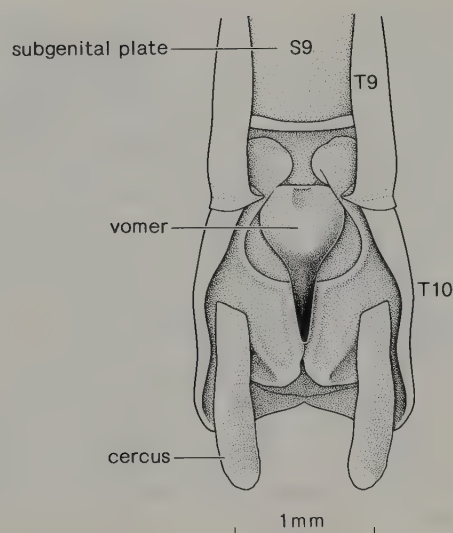


Fig. 25.3 *Parasymploidea granulosa*, apex of abdomen in ventral view, ♂.
[S. P. Kim]

and a number of tubular accessory glands into the short common ejaculatory duct. In the female, the ovaries are composed of free, well spaced, panoistic ovarioles strung along the lateral oviducts and prolonged into fine suspensory ligaments; there is usually a large bursa copulatrix with an independent opening into the genital atrium above that of the common oviduct; accessory glands and single or paired spermathecae may also be present. A pair of glands, which in some species at least have a repugnatorial function, is usually present in the prothorax, opening to the exterior in a notch at the anterolateral angle of the notum. Among Australian species they are known to occur at least in *Extatosoma tiaratum* (see Strong 1975).

Karyotype. The karyotypes studied have $2n\delta$ ranging from 21 to about 100 (M. J. D. White 1976). The higher numbers occur mainly in parthenogenetic species and some of these are polyploid. The male usually has an XO constitution, but XY species are also known (Hughes-Schrader 1959; Scali and Marescalchi 1987). In the Mediterranean genus *Bacillus*, complicated interrelationships exist between karyotype, reproductive isolation, hybridisation, parthenogenesis and polyploidy, with consequences for taxonomy and phylogenetic reconstruction (Scali and Marescalchi 1987).

For the Australian fauna, the karyotypes of 24 species of Phasmatidae (Tropidoderinae, Phasmatinae, Pachymorphinae, Lonchodinae) and Phylliidae (Necrosiinae) were studied by Craddock (1972). She found male diploid chromosome numbers ranging from 26 to 45, with XO and XY sex-chromosome mechanisms. Five species had different chromosome-number races. *Didymuria violescens* had 10, with chromosome numbers from 26 to 40, and *Ctenomorpha chronus* at least 3. In *D. violescens* adjacent races come into parapatric contact, and in some cases hybrids have been found in the tension zones or been produced in crossing experiments (Craddock 1975). In a group of Australian species in the genus *Sipylodea*, *S. similis* has $2n = 35\delta XO, 36\phi XX$, as well as partheno-

genetic females with 57 or 58 chromosomes (possibly polyploid); *S. nelida* has $37\delta XO, 38\phi XX$ and parthenogenetic females with 57, 58 or 69; and *S. ovabditia* $35\delta XO, 36\phi XX$, but no parthenogenetic females (John *et al.* 1987).

Immature Stages

Egg. The eggs (Fig. 25.4) are usually oval or barrel-shaped and show a striking resemblance to seeds. The shell is hard, and may be smooth and shiny, or heavily sculptured in various ways, and sometimes patterned. The anterior pole is truncated and fitted with a variably shaped operculum, which may bear centrally a prominence, the capitulum; dorsally there is a longitudinal, scar-like area, the 'micropylar plate', which strongly resembles the hilum of many seeds and accommodates the micropyle towards its posterior end. The fine structure of the eggs provides excellent taxonomic characters, which are particularly valuable for establishing affinities of obligatorily parthenogenetic species (Mazzini and Scali 1980) and have been applied extensively at both the specific and infraspecific levels (Mazzini *et al.* 1987; Scali and Mazzini 1987 and refs). The Australian species *Sipylodea nelida* and *S. similis* have eggs which when laid are enclosed in two supernumerary membranous envelopes. A few minutes after oviposition these rupture and a system of invaginated tubules in the operculum everts to form a dense cluster of stellate hairs (Fig. 25.5) (John *et al.* 1987). It is remarkable that a closely related species, *S. ovabditia*, entirely lacks this specialisation.

The embryology is described by Beier (1957) and by Bedford (1970, 1978) with special reference to the Australian *Didymuria violescens*. In many species development has an appearance of capriciousness, owing to variability in diapause manifestations resulting from the interaction of genetic and environmental causes. Eggs laid by a single female may produce hatchlings in both the first and second following years, or even in the third, and each hatching period may last for several weeks.

Nymph. Hatching occurs by detachment of the operculum. A 'pronymph', corresponding to that of Mantodea and Orthoptera, does not occur. The nymph (Fig. 25.6B) shows only minor anatomical differences from the adult, involving principally the fewer antennal segments and the rudimentary reproductive organs and wings (in those species possessing them). It undergoes several ecdyses (usually fewer in the male than in the female), hanging in an inverted position from an elevated support; the exuviae are commonly eaten. The wing rudiments and terminalia increase in size from instar to instar, the former not reversing their original orientation as they do in Orthoptera. The number of antennal segments increases by progressive division.

Biology

A general review of the biology and ecology of the Phasmatodea is given by Bedford (1978).

Adults. Most Phasmatodea are apparently rare insects, even allowing for the special features that make detection difficult. On the other hand, a few species may become



Fig. 25.4 Eggs of Australian Phasmatodea: A, *Podacanthus typhon*; B, *Podacanthus wilkinsoni*; C, *Tropidoderus childrenii*; D, *Didymuria violescens*; E, *Ctenomorpha chronus*; F, *Eurycnema goliath*; G, *Ctenomorphodes tessulatus*; H, *Acrophylla titan*; I, *Hyrtacus tuberculatus*; J, *Sipyloidea filiformis*; K, *Pachymorpha squalida*; L, *Extatosoma tiaratum*. [F. Nanninga]

extremely abundant, giving rise to outbreaks or plagues, in which, however, true gregariousness does not seem to be involved. The insects most characteristically frequent the foliage, or sometimes the trunks or stems, of trees and shrubs, but many species are found on plants of the herba-

ceous stratum, or even on litter at ground level. They spend much of their time immobile, often in extraordinary attitudes that must materially assist their procreptic adaptations of structure and colour in deceiving predators. From time to time, especially upon some slight distur-



Fig. 25.5 Egg of *Sipyloidea nelida*, showing stellate hairs. Scale = 1 mm. [SEM Unit, Division of Entomology, CSIRO]

bance, they may perform rhythmical swaying or rocking movements. In locomotion they are generally sluggish and clumsy. They will ascend any vertical support within their field of vision, constantly feeling for new footholds by wide, sweeping movements of the fore legs. In Australia, almost all the species frequenting trees and large shrubs are fully winged, at least in the male. Those found on low herbs are apterous, while those on the lower shrubs and on tall grasses include both types, as well as intermediate ones. Males of fully winged species sometimes fly to lights; most females are flightless. Many stick-insects are largely nocturnal.

When suddenly approached, stick-insects often drop to the ground and lie motionless in a state of catalepsy, which may last for hours if contact with the tarsi is prevented. If the limbs are seized, reflex autotomy may occur between femur and trochanter, at which point the lumen of the leg is almost completely obstructed by a haemostatic diaphragm. When grasped, some species flex their spiny legs spasmodically over the fingers, or raise their wings with a rustling motion. Rarely will any attempt be made to escape by taking to the wing. Bedford and Chinnick (1966) described the defensive responses of the Australian *Eurycnema goliath* and *Tropidoderus*

childrenii, which may be elicited by sharply tapping the metasternum and basal abdominal sterna as the insect hangs from foliage. In *E. goliath* the wings are lifted to display the vivid red undersurfaces of the tegmen and the remigium of the hind wing, together with a pair of eye-like spots on the hind coxae. The widely spread hind legs are rapidly struck together, to the accompaniment of a swishing sound apparently involving the wings. Many species regurgitate the contents of the crop when handled and some are capable of squirting an irritant fluid from the repugnatorial glands of the prothorax. In two such instances (*Anisomorpha buprestoides* and *Megacrania wegneri*) the insects may have an aposematic colour pattern, while in *Anisomorpha* they are at times gregarious. In *Phyllium* spp. and *Extatosoma tiaratum* the 1st instar only is aposematic (p. 402). A few species have been reported as stridulating, by friction between fore and hind wing, or between the enlarged 3rd segments of the antennae. The hind wings are often coloured or mottled on the anal area, while the remigium commonly has a brightly coloured patch, distinctive for the species, in the region covered by the tegmen when the wings are closed.

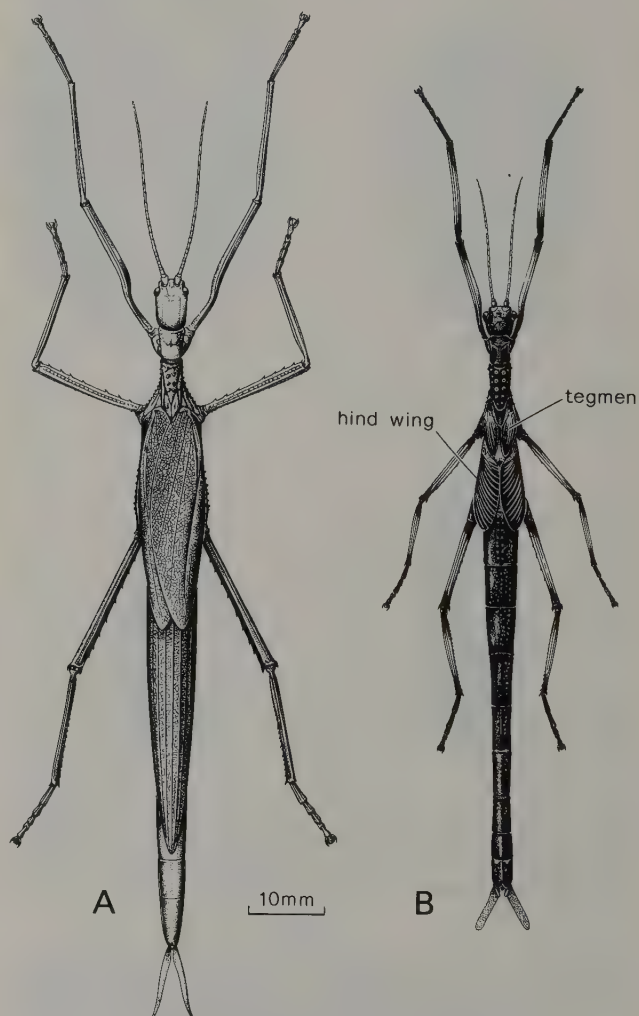


Fig. 25.6 *Podacanthus wilkinsoni*: A, adult ♀; B, last-instar ♂ nymph, high-density phase. [F. Nanninga]

All Phasmatodea feed upon foliage. They are rarely confined to a single host species, but the range of acceptable hosts is commonly limited. In Australia several species feed indifferently upon such divergent genera as *Eucalyptus* and *Acacia*, while most eucalypt feeders accept any species of that genus, at least in the later instars.

Reproduction. In copulation, the male is mounted on the female, with the posterior part of his abdomen curving downward and forward through 180°, so that its ventral face is apposed to the ventral face of the female. The ventroposterior angles of T10 of the male clasp either the base of the female's operculum, or her S7 towards its posterior end, and the intromittent organ is inserted from the side, over the edge of the depressed operculum. Copulation is often prolonged, the sperm being transferred in small spermatophores (J. T. Clark 1975; Carlberg 1981). Detailed structure of the sperm is described by Baccetti (1987c). The eggs are usually laid singly at the rate of one to several per day. Upon leaving the oviduct they may be retained for some time within the ovipositor or the operculum; finally, in most species, they are either passively released, or projected with some force by a sharp flick of the abdomen, and fall to the ground amongst the litter. Some species deviate from this pattern by inserting the eggs into the soil, as in the Australian *Sipyloidea ovabida* (see John *et al.* 1987), or cementing them, singly or in groups, to a support, as in *S. nelida* and *S. similis*. Normal egg production per female seems to range from less than 100 to 1300, according to species.

Parthenogenesis is widespread in the order. In some exotic species, including *Carausius morosus*, it is obligatory, with males unknown or exceedingly rare. More usually it is facultative, unfertilised eggs producing only females; but the parthenogenetic production of males as well as females has been reported (Hadlington and Shipp 1961) for the Australian *Ctenomorphodes tessulatus*.

Nymphs. The nymph on hatching ascends the first upright support it encounters and continues upwards until it finds suitable foliage. At this stage it is dependent upon the softer parts and may have a more restricted host range than the adult. It is vulnerable to desiccation and predators, especially between hatching and establishment on suitable food; in some species hatching occurs in the evening, permitting establishment during the hours of darkness and high humidity. The nymphal stage lasts some weeks or months. Regeneration of damaged or autotomised appendages may occur, so that individuals with short or otherwise abnormal legs are often seen. The behaviour of nymphs is in general closely similar to that of adults; in a few species they are gregarious.

Variation, Colour Adaptation. Marked genetic variation in anatomical features occurs in many species. Horns, thoracic and abdominal spines and granulations, and lobes on abdomen or legs, may be variably developed or absent in the same population. Some species have green and non-green morphs. Many of these characters may also vary geographically, together with overall size and degree of attenuation, relative wing length, and colour of hind wing.

'Morphological' colour adaptation to the background has been recorded in a few species (Bückmann 1977 and refs). More remarkable are the mechanisms of 'physiological' colour change found in *Carausius morosus* and some other species (Giersberg 1928). Darkness and pallor are induced by the migration of dark granules within the epidermal cells. When the granules are clumped together near the basal end of the cells, the insect is pale; when they move distally and spread out to form a continuous curtain, the insect becomes dark. In *C. morosus* there is a diurnal rhythm, the insect being dark at night and pale in the day-time, basically in response to light intensity. Apart from this rhythm, and overriding it, darkening may be induced by about an hour's exposure to low temperature or high humidity, and pallor by the reverse conditions. In the temperature response, the epidermis acts as an independent effector, so that local pallor follows local application of heat to the integument; light and humidity operate through a nervous-endocrine mechanism.

Kentromorphism. Kentromorphic phase differences have been reported (Key 1957) in the Australian phasmatids *Podacanthus wilkinsoni*, *Didymuria violescens*, and *Ctenomorphodes tessulatus*, all of which sometimes reach high population densities. In the nymph, the pro-cryptic low-density phase is rather uniform and usually green, whereas the conspicuous, supposedly aposematic, high-density phase is patterned with black, yellow and sometimes white (Fig. 25.6B). In *P. wilkinsoni* a mean density of one insect per eucalypt branchlet is sufficient to induce the extreme high-density pattern, while the low-density extreme occurs at less than one per 20 branchlets. Intermediate patterns appear at intermediate densities, or in response to density change. All three species also show morphometric phase differences analogous to those of locusts. There is apparently no correlation between density and activity, and no overt gregariousness.

Ecological Features. The rarity of many Phasmatodea may be expected to impose difficulties in the way of sexual contact. These may be offset by the sedentary habits of the female and the behaviour of the young nymph, which tend to ensure that the progeny of a given female will find themselves on the same plant, or on adjacent plants in contact. They may be relieved, also, by the substantial powers of flight of the males of most tree-frequenting species, especially if the female produces a sex-attractant pheromone, as some observations suggest. However, the occurrence of facultative parthenogenesis is an insurance against failure of sexual contact. This view of the situation implies a patchy distribution of the rare species.

It is not known what determines the generally low density of stick-insect populations. Food is usually available in abundance, although the quantity or accessibility of young foliage may be inadequate for the needs of the 1st-instar nymph. On the other hand, in the species liable to outbreaks all edible foliage may be consumed over the greater part of a high-density area. Since the dispersal powers of the insects are low, only those around the fringes survive. Important mortality from predators and parasites is suffered in both the egg and active stages. Fire

must have drastic effects, its severity and time of incidence determining whether it will disadvantage principally the phasmatids or their natural enemies (Campbell 1961).

Although human modification of the habitat may have increased the frequency and severity of outbreaks, yet the capacity for kentromorphic change that has been evolved in all three of the Australian plague species indicates that they have always been subject to recurrent high density. In *Podacanthus wilkinsoni*, *Didymuria violescens* and the American *Diapheromera femorata*, outbreak densities are usually reached only every alternate year over an outbreak period, the incidence of high density having somehow come into relation with the predominantly two-year life cycle, perhaps through the proportionately greater pressure of predation on the low-density broods (Readshaw 1965).

Natural Enemies. The procryptic adaptations and other defensive mechanisms of all stages of Phasmatodea are probably directed mainly against bird predators. In Australia, Readshaw (1965) states that large nymphs and adults of *Didymuria violescens* form at times the principal food of such birds as *Strepera graculina* (pied currawong), *Coracina novaehollandiae* (black-faced cuckoo-shrike) and *Anthochaera carunculata* (red wattle bird). Young nymphs are subject to attack by small birds,

and also by ants (*Myrmecia* and *Iridomyrmex* spp.) and probably spiders. Eggs are eaten by a number of general predators on the forest floor, including ants, birds, and marsupial mice (*Antechinus* spp.).

Parasitism is also frequent. The active stages are attacked by parasitoid tachinid flies, while erythraeid mites of the genus *Charletonia* are sometimes abundant as ectoparasites. The eggs are extensively parasitised by minute amisegine wasps (Chrysididae). In Australia several species are involved, mainly in the genus *Myrmecomimesis*. The wingless female wasp chews a hole in the thick shell of the egg and deposits her own egg through this.

Economic Significance. Only a few species are rated of economic importance. In Australia, *Podacanthus wilkinsoni*, *Didymuria violescens* and, to a less extent, *Ctenomorphodes tessulatus* are responsible for extensive defoliation of eucalypt forests. Some of the most valuable timber species are especially sensitive, a single defoliation causing a high percentage of deaths in both *Eucalyptus regnans* and *E. delegatensis*. Even moderate defoliation causes reduction in growth increment. Repeated defoliations have led to accelerated soil erosion on steeply sloping catchments. Papers on the biology of the three pest species are listed by Readshaw (1965) and Bedford (1978).

CLASSIFICATION

Order PHASMATODEA
(ca. 150 Australian spp.)

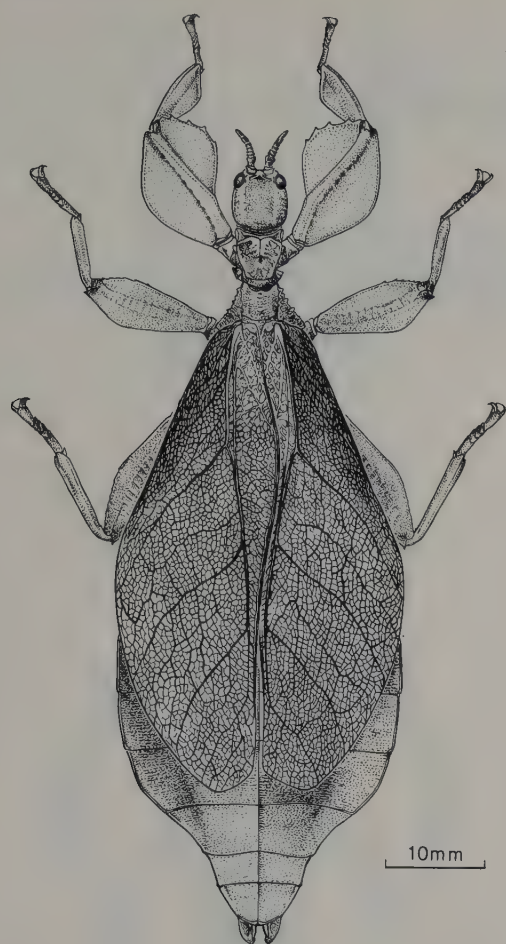
1. Phylliidae (ca. 55)
2. Phasmatidae (ca. 95)
- Timematidae (0)

The modern classification of the Phasmatodea may be said to date from Günther (1953). It was followed virtually without change for some 20 years. This stability was upset by the reclassification of Bradley and Galil (1977), who proposed rank escalations and other changes while rarely stating grounds for them. Kevan (1977b) took this process considerably further and five years later (Kevan 1982) proposed still other substantial changes, in both cases with little or no stated grounds. However, Kristensen (1975) had pointed to two areas where features of the insects themselves could justifiably call for changes to the classification. These were the unsatisfactory status, as a character, of the *area apicalis* of the mid and hind tibiae, and the very aberrant features of the Nearctic genus *Timema*. The second had in fact been recognised by Essig (1926) in establishing the family Timematidae (as 'Timemidae'), with priority from Caudell (1903) as Timeminae. Key (1974a) pointed out that the Necrosciinae, placed in the Phasmatidae by Günther (1953), have a well developed vomer remarkably similar to its counterpart in *Phyllium* and other Phylliidae and proposed the transfer of that subfamily to the Phylliidae. If the presence of a vomer were to be used in place of the *area apicalis* as the diagnostic character of the Phylliidae, transfer of some genera at present referred

to Lonchodinae and Phibalosomatinae would also be required.

Here the classification of Günther is followed, but with the addition of the Timematidae as a third family, the inclusion of the Necrosciinae in the Phylliidae, the replacement of Günther's name Podacanthinae by its senior synonym Tropidoderinae, and the reallocation of a few genera. The Timematidae are exclusively North American. The Phylliidae and Phasmatidae are both widely distributed in the warmer parts of the world; both exhibit an extraordinary diversification in body form and integumental processes, many of the trends showing marked parallelism. In Australia only two or three subfamilies of the Phylliidae are represented, but eight out of 10 of those of the Phasmatidae. More than half of about 50 genera, and nearly all the species, are endemic, but none of the subfamilies. Vickery (1983) has catalogued the named Australian Phasmatodea.

1. Phylliidae. As here understood, the Phylliidae comprise eight subfamilies, of which the Phylliinae and Necrosciinae are represented in Australia. There is also an early record of the genus *Haaniella* (Heteropteryginae). The PHYLLIINAE, or 'leaf insects', in which the body is strongly flattened dorsoventrally and the abdomen and

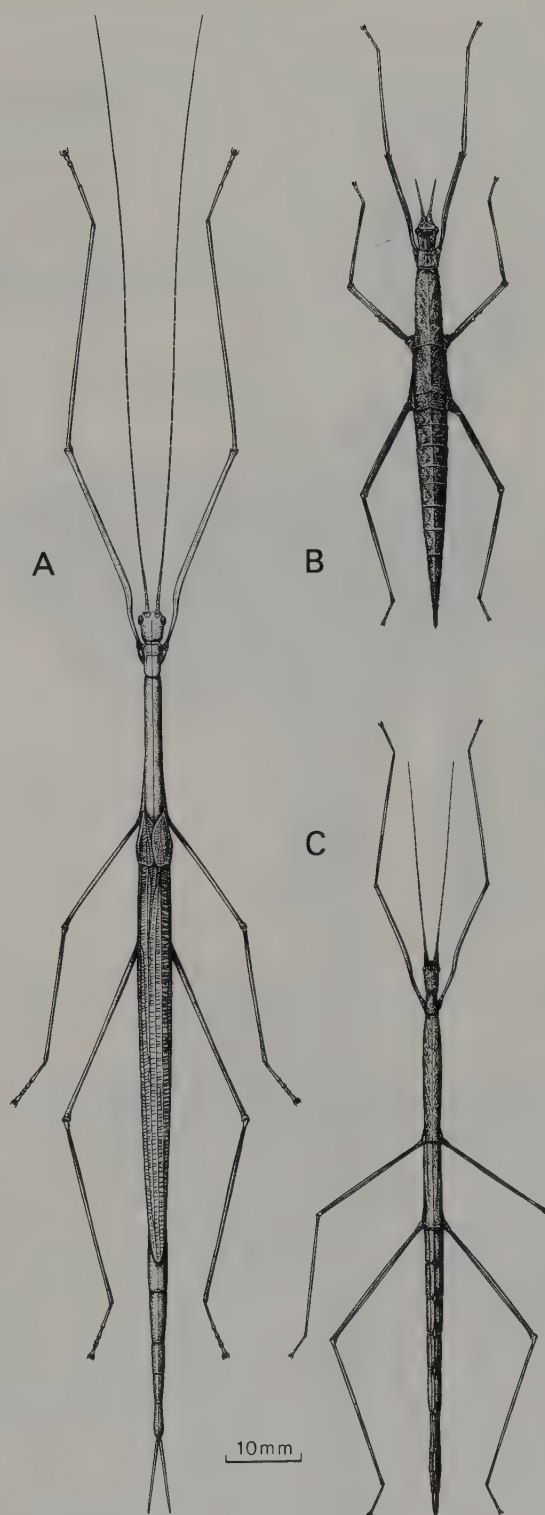
Fig. 25.7 *Phyllium siccifolium*, ♀.

[S. Monteith]

legs bear broad lamellate expansions, occur widely in South-East Asia and New Guinea. In Australia they are represented by at least three species, in the genera *Phyllium* and *Nanophyllium*, in the rainforests of northern Qld. In the female the antennae are very short and the fore wings cover almost the whole of the body, while the hind wings are greatly reduced (Fig. 25.7). The NECROSCIINAE are a large, principally South-East Asian group of medium-sized phylliids, with long slender antennae and very small fore wings (in the winged forms). In Australia the winged genus *Sipyloidea* (Fig. 25.8A) has a number of species frequenting tall tropical grasses, and others, with brachypterous females, found on shrubs in the arid parts of southern Australia. *Parasipyloidea*, with many apterous species, occurs on plants of the herbaceous stratum in eastern Australia.

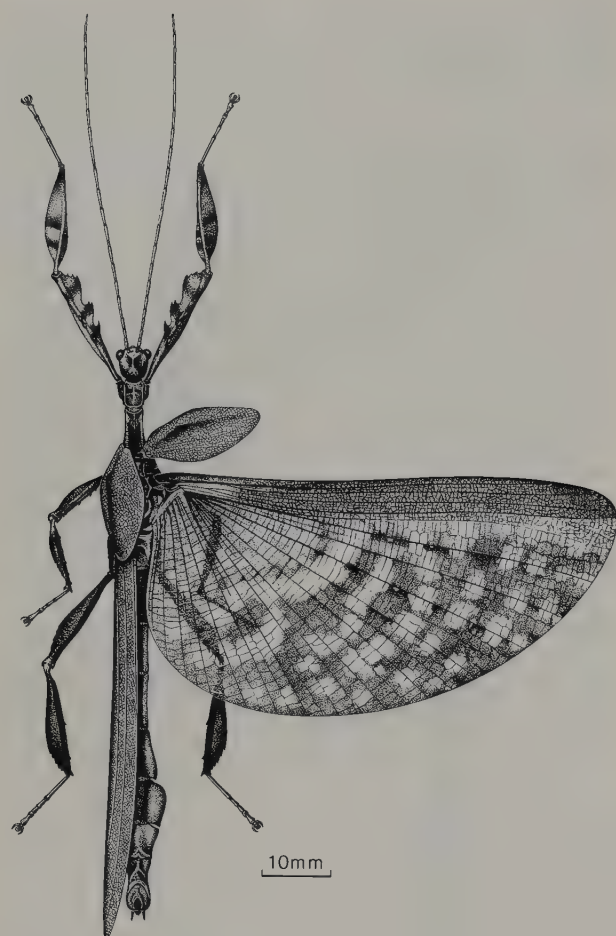
2. Phasmatidae. Günther (1953) gives keys to the subfamilies. The taxonomy and nomenclature of the injurious Australian species and some of their allies have been discussed by Key (1957, 1960).

The subfamily TROPIDODERINAE is the most characteristically Australian group, with a continent-wide distribution. It comprises mainly large, winged species, which resemble leaves rather than twigs, although they are not markedly flattened. *Podacanthus* includes four species

Fig. 25.8 A, *Sipyloidea filiformis*, ♀; B, *Pachymorpha squalida*, ♀; C, *Hyrtacus tuberculatus*, ♀.

[F. Nanninga]

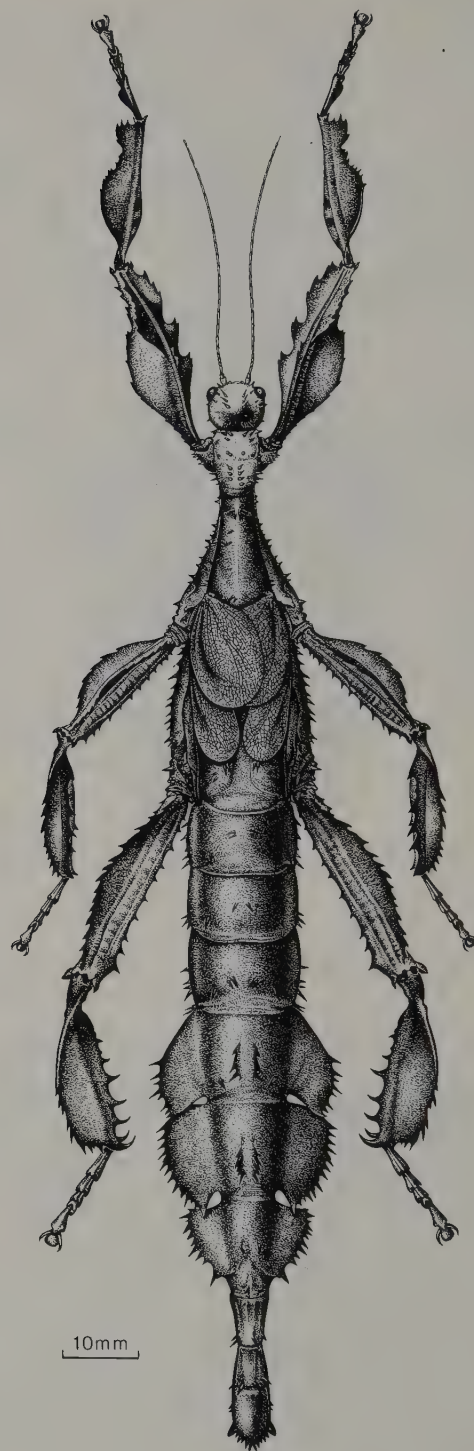
(with rather regularly spined mesonotum, long cerci, and fully winged females), of which two are injurious. *P. wilkinsoni* (Fig. 25.6A) is distinguished by the orange-yellow proximal patch on the remigium of the hind wing. *Extatosoma tiaratum* (Figs 25.9, 10; see Gurney 1947) is

Fig. 25.9 *Extatosoma tiaratum*, ♂.

[F. Nanninga]

remarkable for the numerous spines and integumental expansions on the body and legs, including a tuft of spines on the conical occiput of the hypognathous head. The male has large mottled wings, while the female is heavy-bodied and brachypterous. The insect often hangs inverted amongst foliage, with its highly procryptic abdomen curled over its back. The 1st instar has an aposematic pattern of black, with orange head and whitish collar; in its colouring, posture and movements it appears to mimic ants of the genus *Leptomyrmex*. *Didymuria violescens* (Fig. 25.11) is fully winged in the male, which has inflated hind femora bearing two or three large black spines ventrally; the female is shorter-winged and flightless, with the hind femora unspecialised.

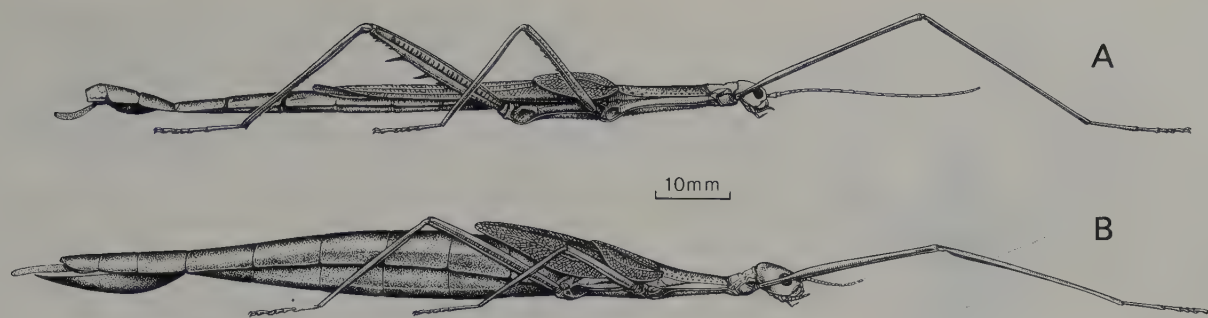
The PHASMATINAE are another prominent group with an Australia-wide distribution. The species are mainly large, winged and stick-like. *Ctenomorphodes tessulatus* (Fig. 25.12) is a medium-sized, slender phasmatid, with spiny mesonotum and strongly tessellated hind-wing pattern. The males are fully winged, the females short-winged and flightless. The longest Australian phasmatid, which reaches a body length of 25 cm, is the spiny *Acrophylla titan* of the eastern coast, with large mottled wings in both sexes and wavy-margined, three-ridged cerci. Somewhat

Fig. 25.10 *Extatosoma tiaratum*, ♀.

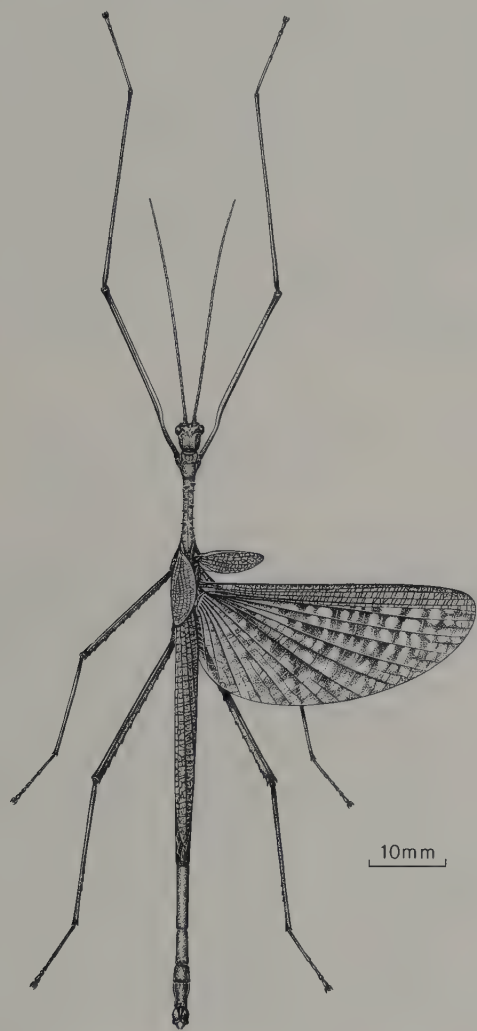
[F. Nanninga]

shorter, but more heavily built, is the mainly tropical *Eurycnema goliath*, in which the female is conspicuously banded with green and yellow, with the fore wings and the remigium of the bluish-veined hind wings a bright red beneath.

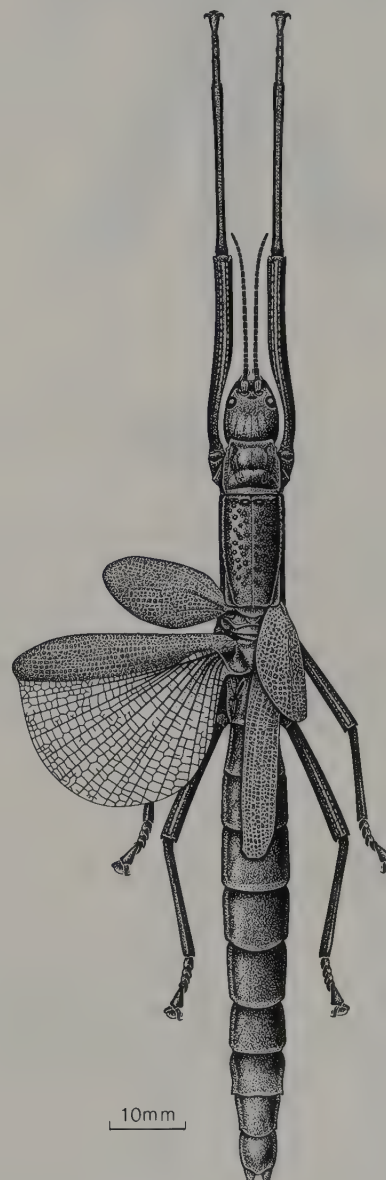
The PLATYCRANINAE, occurring mainly on the islands to the north of Australia, have one Australian representative,

Fig. 25.11 *Didymuria violescens*: A, ♂; B, ♀.

[F. Nanninga]

Fig. 25.12 *Ctenomorphodes tessulatus*, ♂.

[F. Nanninga]

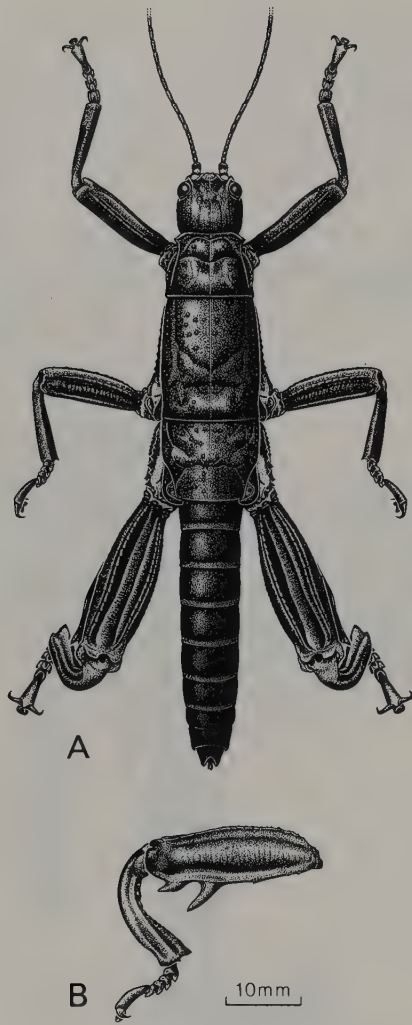
Fig. 25.13 *Megacrania batesii*, ♀.

[S. P. Kim]

Megacrania batesii (Fig. 25.13), living on *Pandanus* in north-coastal Qld and also recorded from the Pellew islands in the Gulf of Carpentaria.

The EURYCANTHINAE are mainly Papuan in distribution, but a few species have been recorded from the Cape York area, including a *Eurycantha* from Thursday I. However, the most interesting Australian representative is the possibly extinct *Dryococelus australis* (Fig. 25.14). This is a

shiny, heavy-bodied, reddish brown, wingless species, the male having enormously thickened hind femora with a few heavy spines beneath (Gurney 1947). It was formerly



very abundant on Lord Howe I., where it frequented large cavities in the trunks of living trees, coming out at night to feed. It has been exterminated on the main island by rats, which were accidentally introduced in the early part of the century, but may still occur on an associated small island known as Ball's Pyramid (Smithers 1969).

The subfamily XERODERINAE, also mainly Papuan and Melanesian in distribution, is represented by two little-known species from Qld. The African PALOPHINAE also have two or three Australian outliers.

The PACHYMORPHINAE are rather small, dun-coloured, apterous phasmatids with short antennae, of which *Pachymorpha*, with several species (Fig. 25.8B), is widespread in Australia. The insects are usually found on the lower part of tree trunks, or on ground litter around their base.

A subfamily of particular interest in Australia is the apterous LONCHODINAE, which are widely distributed over the continent, as well as in New Guinea and South-East Asia. They frequent plants of the herbaceous stratum, or low shrubs. Several exceedingly slender ones occur on tall tropical grasses, or on the hummocks of arid spiny grasses of the genus *Triodia*. In *Hyrtacus* (Fig. 25.8C) the female supra-anal plate is more or less elongate, but clearly separated from T10. In *Marcenia* it is elongate and fused to that tergum.

Fig. 25.14 *Dryococelus australis*, ♂: A, dorsal; B, hind femur, lateral.

[S. P. Kim]

Embioptera

Embiidina

(*Embiids, web-spinners, foot-spinners*)

E. S. ROSS

Mandibulate exopterygote Neoptera, with apterous females and winged or apterous males; living in silken galleries; fore basitarsi globose.

The Embioptera (or Embiidina, as this author prefers) comprise one of the smaller, lesser-known orders of insects. Like their distant relatives, stick-insects, termites and earwigs, embiids are essentially tropical, but some species occur in warm-temperate climates. The order is well represented throughout Australia, two species even occurring above 2000 m in the Australian Alps. Less than 200 species are recorded for the world, but recent field work indicates that as many as 2000 may exist. Because of almost complete confinement of activity to their silk galleries (Fig. 26.5), embiids are seldom seen by the non-specialist, except for alate males attracted to light. They are small to medium-sized, narrow-bodied insects (Fig. 26.1), easily recognised by the greatly swollen fore tarsi which are packed with silk glands. They may be aberrant derivatives of the orthopteroid stem group, owing their persistence to the survival potential afforded by life in silk galleries.

The Australian fauna has been described by Tillyard (1923a), C. Davis (1936–44, 1944a) and Ross (1963), while Barth (1954) has given an excellent account of silk production. Ross (1970) reviewed the biosystematics of the order.

Anatomy of Adult

Head (Fig. 26.2). Strongly prognathous, always with a sclerotised gular bridge between submentum and occipital foramen. Antennae filiform, 12–32-segmented. Eyes reniform, compound, often large in male, always small in

female; ocelli absent. Mandibles of adult males usually flattened, elongate, often with only a few inner-apical dentations. Submentum of males often large, sclerotic, shield-like.

Thorax. Female without even rudimentary wings; ventral thoracic sclerites separated by membrane. Apterous males with thorax similar to that of females, or with short

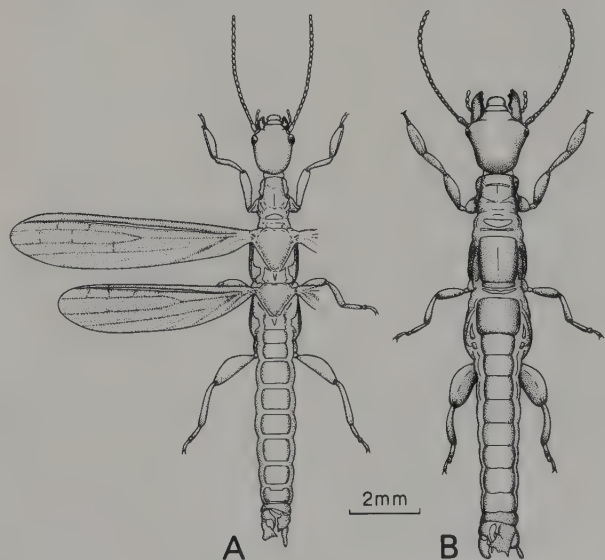


Fig. 26.1 Adult embiids, dorsal: A, *Notoligotoma nitens*, Notoligotomidae, ♂; B, *Metoligotoma* sp., Australembiidae, ♂. [B. Rankin]

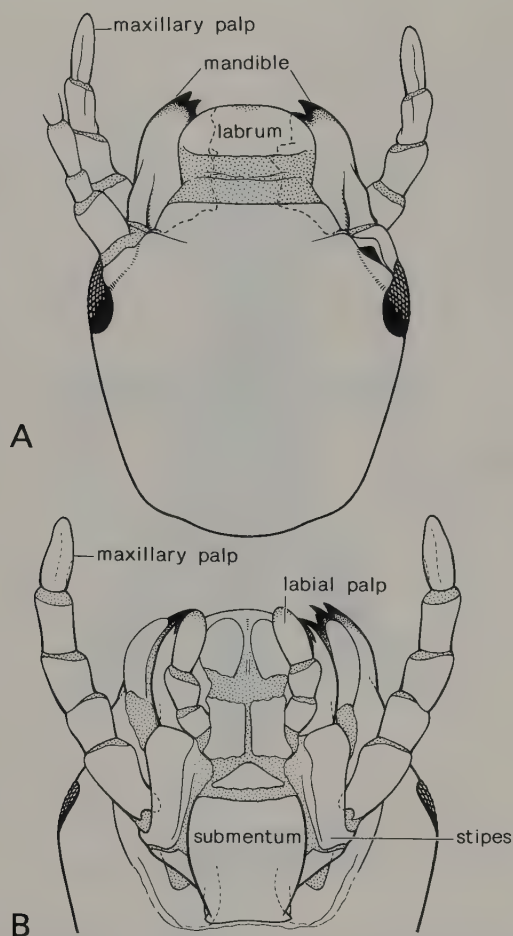


Fig. 26.2 Head of *Australembia incompta*, Australembiidae: A, dorsal; B, ventral. [E. S. Ross]

wing buds. Pterothorax of winged males flattened, rigid; nota triangular; axillary cords very long; scutellum small; ventral sclerites fused.

Legs. Very short; tarsi 3-segmented; basal segment of fore tarsus distended by silk glands (Fig. 26.4); mid legs relatively small; hind legs with enlarged femora due to large size of tibial depressor muscles.

Wings. Elongate, subequal; with characteristic, pigmented stripes alternating with hyaline stripes. R_1 a broad, inflatable blood sinus (RBS) with granular, pink borders; most other veins normal or represented only by a line of setae and pigment stripe; basal half of R_s and MA closely parallel, appearing as one vein; cubitus developed as a blood sinus (CuBS) from which emerges CuA ; an anal blood sinus (ABS) represents the rudimentary anal vein; few cross-veins (Fig. 26.3).

Abdomen. Elongate, with 10 well-defined, subequal segments; cylindrical in female, dorsoventrally flattened in male; cerci 2-segmented, tactile. External female genitalia represented only by slightly modified S8 and S9 and rudimentary valvifer lobes. Male genitalia (Fig. 26.6) complex, asymmetrical; T10 cleft, bearing complex processes and flaps; left cercus enhanced by lobes and/or by segment-fusion to better function as a clasper in copulation.

Internal Anatomy. Alimentary canal simple, with large salivary glands and 6 rectal papillae; 20–30 Malpighian tubules in adult. Nervous system with 3 thoracic and 7 discrete abdominal ganglia. Reproductive system with indications of a segmental arrangement in the 5 pairs of serially arranged panoistic ovarioles in the female and 5 pairs of testes in the male. The tarsal silk glands are described below.

Immature Stages

The eggs are elongate and with a rimmed, circular operculum. Nymphs are similar to adult females, but those of males destined to have wings develop external wing pads.

Biology

The outstanding feature of embiids is an ability to spin galleries of silk with their fore tarsi. The silk glands contained in the enlarged basal tarsal segment are irregularly shaped globules tightly packed like seeds of a pomegranate fruit, as many as 200 occurring in a single tarsus (Fig. 26.4). Each gland is a single layer of syncytial cells enclosing a large lumen which stores the liquid silk secretion of the gland wall. Single ducts conduct the secretion to hollow, seta-like ejectors on the ventral surface of the tarsus, where it issues spontaneously as the ejectors brush against a surface. The spinning action of the fore legs resembles the movements of a shadow boxer, and embiids, unless the temperature is too low, constantly extend their galleries to new food sources, or add silk layers to older galleries. Freshly-spun galleries are often blue-white or violaceous, but old, multilayered silk is chalk-white.

The distinctive, enlarged fore tarsi serve as a universal recognition feature of the order in all stages of the life history. It is remarkable that even 1st instar nymphs spin silk, and that the ability is life-long. In most insects silk production seldom extends into the adult stage.

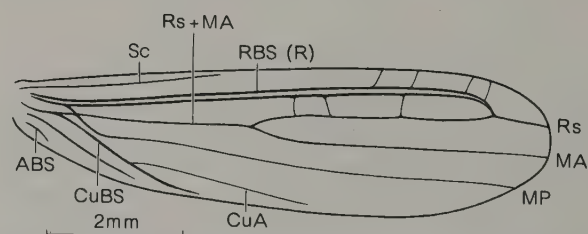


Fig. 26.3 Venation of fore wing of the oligotomid type characteristic of all alate Australian Embioptera; *Aposthonia* sp. of *gurneyi* complex, Oligotomidae. [E. S. Ross]

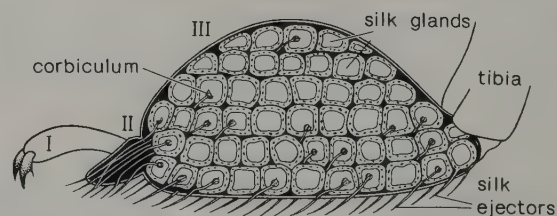


Fig. 26.4 Longitudinal section of fore tarsus, showing silk glands and ejectors, schematic. [E. S. Ross]

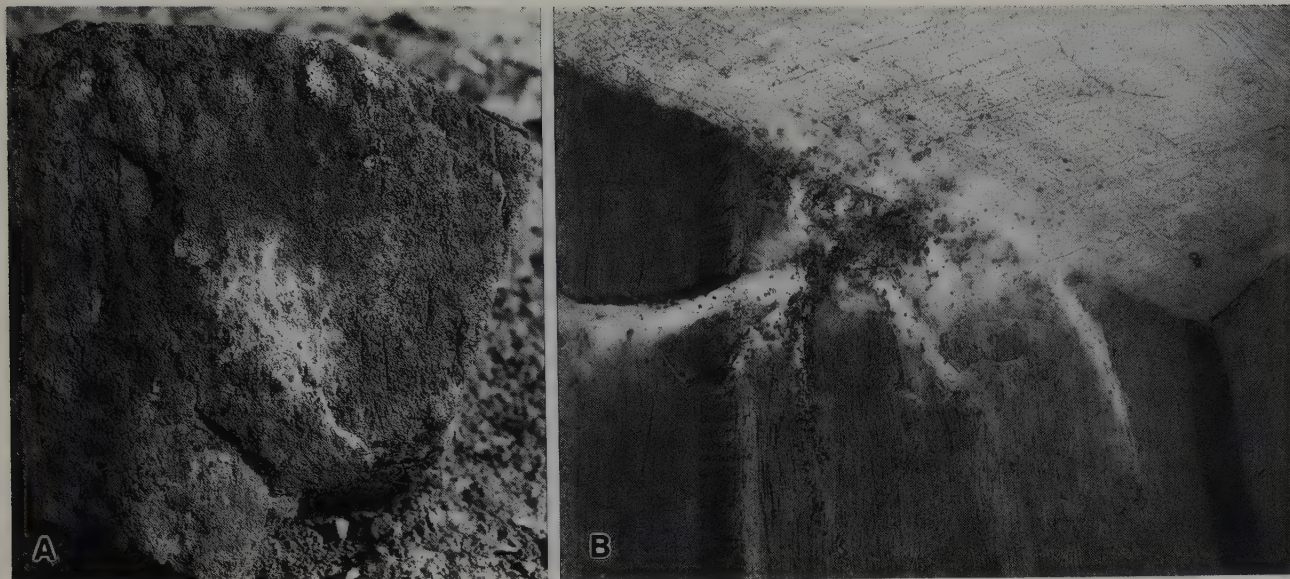


Fig. 26.5 Galleries of: A, *Aposthonia* sp. of *approximans* group, Oligotomidae, extending up from soil retreat to lichen food source on exposed rock surface on desert hillside, W.A.; B, *Notoligotoma hardyi*, Notoligotomidae, female nest on old fence near Perth, W.A. [E. S. Ross]

As an embiid spins, it rotates its body and forms a silken tube narrow enough to permit constant contact of its body hairs with the gallery wall. In humid regions, many species produce exposed galleries on bark and rock surfaces, but others hide themselves in crevices and bark flakes with little exposure of silk. In some species faeces and masticated vegetable fragments are added to silk surfaces to provide additional cover, but in others the surface may be bare. In dry regions, heat, desiccation and bush fires are evaded in galleries penetrating cracks in the soil (Fig. 26.5A), crevices in rock or termite mounds, or ramifying beneath stones. Some species live in old fence posts (Fig. 26.5B) or in leaf litter. In tropical cloud forests up to 4500 m, hanging moss is often an embiid habitat.

All distinctive features of embiids—the elongate, supple body, short legs, prognathism, aptery, efficient reverse locomotion, peculiar wings, and sensitive cerci—are adaptations to life in silk galleries. The galleries are as much an embiid element as water is to fish. The universal similarity of the gallery interior explains why embiids display no great range of general form and habits, in spite of great evolutionary age.

The galleries are coverways for all embiid activity except dispersal. They provide predetermined routes of rapid escape from predators, such as ants, which most often are encountered at the periphery of the galleries. At such times an embiid darts backward with great rapidity, while the predator makes a usually unsuccessful pursuit outside the gallery. The exceptionally large depressor muscles of the hind tibiae motivate this reverse movement, while highly sensitive cerci function as tactile caudal 'eyes'.

The food of embiids is entirely vegetable, consisting of outer bark, dead leaves, living moss, and lichens. A ready source of food is likely to be present wherever embiids choose to live on the basis of other ecological factors.

They are easily cultured in tubes or jars containing habitat material.

Originally embiids were alate in both sexes, but the stiff wings of ancestral forms must have slowed reverse movement by producing friction or snagging against the gallery wall. Through selection these became flexible and able to fold back at any point to reverse the axis of friction. Wings of modern embiids, when laterally extended for flight, are temporarily stiffened by blood pressure in the blood sinuses—particularly that of the radius (RBS). To produce eggs and guard the young necessitates a prolongation of life in females, and consequent longer exposure to the selective pressures of gallery life. Thus, past possession of wings by females was disadvantageous in spite of their flexibility. It may be that all modern adult female embiids are wingless as a result of selection for arrested development at a stage comparable to 3rd-instar nymphs, and neoteny would also have led to elimination of protruding genitalia. Size increase continued, however, and females are generally larger and more robust than males.

Aptery, either by neoteny or by brachyptery, occurs in males of certain species, especially those inhabiting arid or marginal environments. In some genera alate males are unknown, but usually only certain species of a genus are apterous, while in others both apterous and alate males occur in the same population or brood.

Embiids are often regarded as subsocial insects. Actually, they are simply gregarious, without castes or division of labour. In some species cannibalism occurs unless each nymph leaves the parent colony and develops independently. Males of such species are usually consumed by the female after mating. However, a typical colony consists of one or more adult females living in the midst of their broods which create and share a common labyrinth of galleries. Adult males are short lived, and

usually take no food. Their distinctive mandibles are adapted for grasping the head of the female during copulation.

Reproduction. After mating, the female starts a new colony, or an extension of an old one, by utilising a protected portion of the colony as a retreat and depositing a layer of eggs on a silk-enclosed surface. Often the eggs are coated by, or embedded in, a hardened paste of masticated bark, leaf fragments or faeces. In some species they are naked, laid singly or in clusters, and moved about in the gallery in the manner of ant eggs. The parent female guards her eggs and newly hatched young, but these soon spin small galleries to fit their body size.

Natural Enemies. As long as embiids remain in their galleries they are relatively safe from free-roving predators, but the predation hazard greatly increases during even short movements in the open to seek new habitats. Within the galleries the embiids have a variety of natural enemies. Scelionid wasps parasitise the eggs; ectophagous larvae of chrysidoid wasps (Sclerogibbidae) feed on developing nymphs; tachinid fly larvae and eugregarine Sporozoa are internal parasites; and, in certain regions, tiny cimicoid Hemiptera of the family Plokio-philidae (not known from Australia) infest the galleries and suck the blood of the embiids. There is also the usual hazard of mites and of viral and bacterial disease.

Economic Significance. Because of their preference for dead vegetable food and uncultivated habitats, embiids are of practically no economic importance. Only occasional minor economic records, such as the webbing of grape bunches or colonisation of a sugar refinery, have been reported. A few species, particularly Indian species of *Oligotoma*, have become widespread through ancient and modern commerce.

Special Features of the Australian Fauna

Embioptera are best represented on the great continental land masses of the tropics. Perhaps because dispersal is slow and limited by aptery of females, the order is sporadically distributed and very poorly represented on islands. Even such insect-rich islands as New Guinea and the Philippines have only related species-complexes of a single genus (*Aposthonia*). Australia, however, though peripheral to embiid centres, has an interesting fauna developed from three basic stocks, which were undoubtedly gained by way of land connections with South-East Asia, while perhaps some species have moved southward from New Guinea by way of a Torres Strait connection. Two species have recently been introduced in commerce. Apparently, the order has not reached New Zealand, and it is absent from Chile and Patagonia.

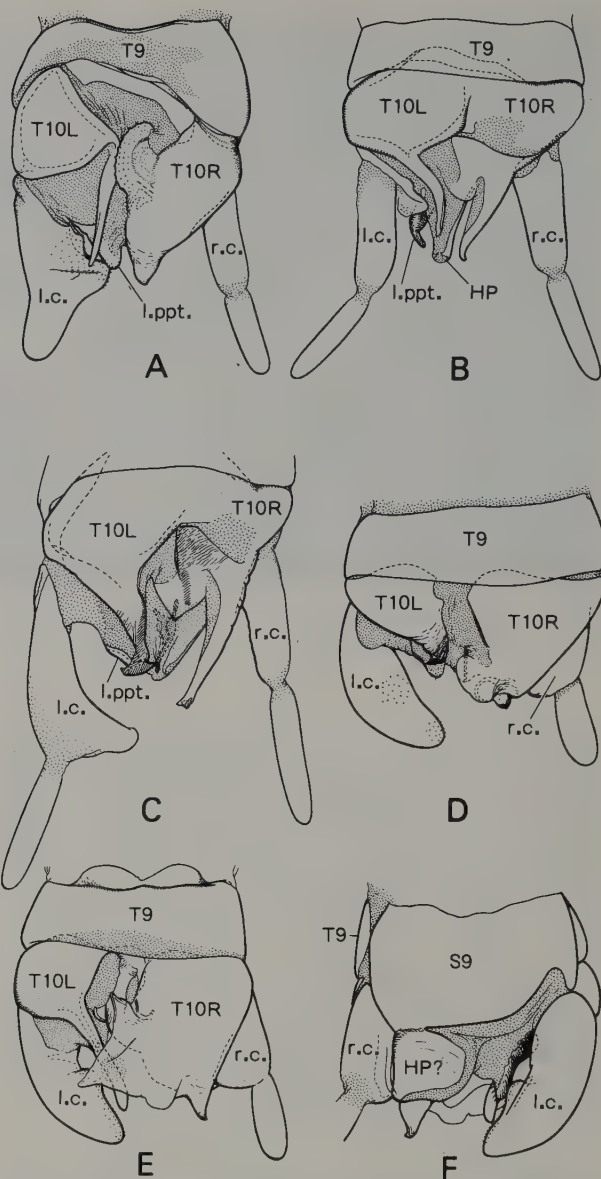


Fig. 26.6 Male terminalia (dorsal, except F) of: A, *Notoligotoma hardyi*, Notoligotomidae; B, *Oligotoma nigra*, Oligotomidae; C, *Aposthonia glauerti*, Oligotomidae; D, *Australembia incompta*, Australembiidae; E, *Metoligotoma illawarrae*, Australembiidae; F, *M. illawarrae*, ventral. [E. S. Ross]

T10L, T10R, left and right hemitergites of T10; l.c., r.c., left and right cerci; l.ppt., left paraproct (the right paraproct is atrophied); HP, caudal process of S9 (hypandrium).

As may be expected in a tropically centred group, there is no evidence of faunal exchange through southern connections.

CLASSIFICATION

Order EMBIOPTERA (65 Australian spp.)

- Clothodidae (0)
- Embiidae (0)
1. Notoligotomidae (6)

- Embonychidae (0)
- Anisembidae (0)
2. Australembiidae (32)

- Teratembidae (0)
3. Oligotomidae (27)

There are also several new family-group taxa to be established in other faunas of the world.

Due to character reduction in females resulting from neoteny, the classification of embiids must be based on adult males. The most important characters are head structure, hind basitarsal sole-papillae, and, above all, the

complex abdominal terminalia. Females and nymphs without associated adult males can be identified only when the fauna of the particular area is well known. Many of the species-complexes of the Australian fauna tend to form geographic races.

Key to the Families of Embioptera Known in Australia — Adult Males

1. Left cercus with terminal segment normal, clearly delimited by a membranous joint, basal segment often inwardly lobed but never echinulate; hind basitarsus with only 1 (terminal) ventral papilla **Oligotomidae**
Left cercus with terminal segment partially or entirely combined with basal segment, the composite segment with one or more echinulate inner areas or lobes; hind basitarsus usually with 2 ventral papillae 2
2. Usually winged; if apterous, basal segment of right cercus elongate and similar to the terminal segment; S9 of abdomen (hypandrium) continuously produced caudally as a subgenital lobe (HP) **Notoligotomidae**
Always apterous; basal segment of right cercus very short, hemispherical; S9 with caudal margin transverse, and with a nearly completely detached, large, triangular sclerite (HP?) on its right caudal half **Australembiidae**

1. Notoligotomidae. The one Australian genus, *Notoligotoma* (Fig. 26.1A), is most closely related to *Ptilocerambia* of south-eastern Asia. *N. hardyi* and a complex of related species or races occur in south-western Australia, usually on the undersurfaces of exfoliated rock slabs on granitic outcrops of arid regions. In Perth, *N. hardyi* is common in crevices of old board fences in residential areas (Fig. 26.5B). The large, pale, winged males fly to light during the first rains of the cold season in May. Species or races related to *N. hardyi* are also common in dry bark or on rock surfaces in the drier zones of northern Qld. Lichens are the preferred food of *Notoligotoma*, and the species never use soil as a habitat. *N. nitens* occurs as a complex of races from Vic. northward into Qld, inhabiting lichens of ledges, bark flakes and old fence posts. Unlike pale *N. hardyi*, *N. nitens* adults are glossy jet-black; the males are either apterous or alate.

2. Australembiidae. This family, known only from eastern mainland Australia and Tas., is the only peculiarly Australian element of the order. Both males and females are entirely apterous. The most important family character is the semi-detached, triangular, ventral lobe of the right caudal margin of S9 in the male. The male cranial and mouth-part anatomy (Fig. 26.2) is also unusual. The left cercus of the male is always 1-segmented, and the rudiment of the terminal segment is not projected as a lobe as in *Notoligotoma*. *Australembia* (2 spp.) has only

one hind basitarsal papilla, and the males have massive maxillary palps and a peculiar, elongate submentum; *A. rileyi* and *A. incompta* are found in leaf litter in savannah zones of North Qld. *Metoligotoma* (Figs 26.1B, 7) is a large complex of closely related species and races with robust apterous males similar in appearance to those of *Australembia*, but having 2 hind basitarsal papillae, normal palps, and usually a soft, transverse submentum. All species live in leaf litter, and range from the Central Qld coast southward into Tas. Most occur east of the Great Dividing Range, and one species has been found above 2000 m in the Australian Alps.

3. Oligotomidae. This family includes Australia's most widespread embiid genus, *Aposthonia*, which also occurs throughout tropical Asia and the eastern Pacific area. In eastern Australia the principal species complex is *A. gurneyi*, found mostly in bark, post and rock crevices, and amongst lichens. The genus has its greatest diversity of species in W.A. A small black species in North Qld is one of the smallest of the order, averaging only 5 mm in length. Many western species live in soil crevices, with no surface galleries evident except briefly after rains. Males frequently fly to light. *Oligotoma* is an Indian genus represented by the introduced species *O. saundersii* in Qld and *O. nigra* from inland N.S.W. Both may be expected to extend their range steadily in Australia, as they have in many other regions of the world.



Fig. 26.7 *Metoligotoma* sp. of *reducta* complex, Australembiidae, male. Length ca. 10 mm.

[E. S. Ross]

Zoraptera

C. N. SMITHERS

Small exopterygote Neoptera; with moniliform antennae; Y-shaped epicranial suture; mandibulate mouth-parts; tarsi 2-segmented; wings, when present, membranous, with reduced venation, aptery common; cerci short; females with ovipositor greatly reduced or absent.

This is an order of about 30 described species of one genus, *Zorotypus* (Fig. 27.1), recorded from the Ethiopian, Oriental, Nearctic, Neotropical and Pacific regions. Zoraptera have not been found in Australia, and reports of their occurrence in New Guinea have not been substantiated; however, the group was recently collected on Christmas Island (Indian Ocean). They are less than 3 mm long, poly-morphic, and have been found living gregariously under bark, in rotten wood and in termites' nests. There have been two schools of thought about their relationships, one associating them with the Psocoptera (i.e. with the hemipteroid orders), the other with the blattoid-orthopteroid orders. The head and mouth-parts are more blattoid than hemipteroid and the structure of the thorax is reminiscent of that of the thorax of the Isoptera. The presence of cerci is a blattoid feature; they are lacking even in fossil psocids. The male genitalia of Zoraptera also appear to be blattoid. On the other hand, apparent hemipteroid features in the internal anatomy and the superficial resemblances to psocids could be the result of convergence. The weight of evidence strongly suggests blattoid associations.

Useful accounts of the order have been given by Tillyard (1926c), Gurney (1938), Bolivar y Pieltain and Coronado-G (1963), New (1978b) and Poinar (1988).

Anatomy of Adult

Head. Hypognathous; epicranial suture distinct; anten-

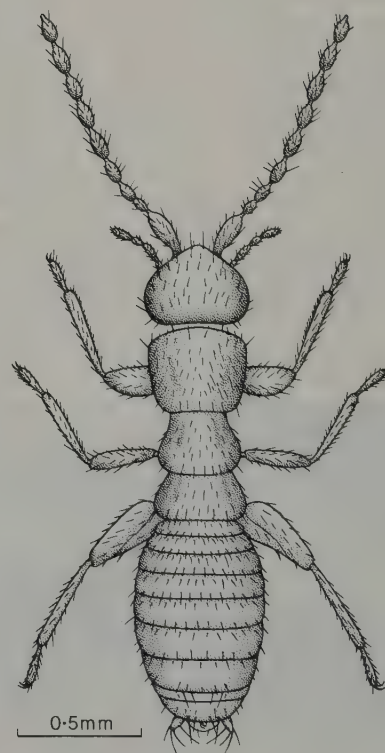


Fig. 27.1 *Zorotypus hubbardi*, apterous ♂, U.S.A.

[B. Rankin]

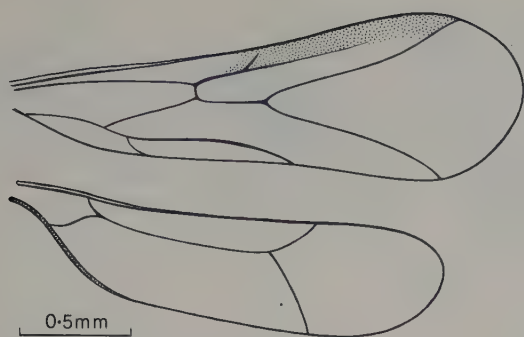


Fig. 27.2 Wing venation of *Zorotypus hubbardi*.

[S. Smith]

nae 9-segmented; mandibles strong, the left bearing a group of hairs; maxillae with lacinia fused to stipes; palps 5-segmented; labium with divided prementum, palps 3-segmented.

Thorax. Prothorax well developed, with undifferentiated notum; pterothoracic terga of winged forms with differentiated prescutum, scutellum and postnotum; apterous forms with simple terga. Pleura of alates and apterous forms essentially similar and with usual sclerites recognisable but with a differentiated lateropleurite and laterosternite in the alates; apterous forms with pleural suture oblique, anteriorly displaced dorsally. Sterna broad, inter-segmental membranes extensive.

Legs. Coxae large, femora fairly stout, tibiae cylindrical, 1st tarsal segment shorter than 2nd.

Wings. Hind wings smaller than fore wings; venation of both simplified (Fig. 27.2). The wings can be shed at basal fractures, the stumps remaining.

Abdomen. Eleven-segmented, with unsegmented cerci.

The male genitalia often asymmetrical but the homologies of their parts are obscure. Delamere-Deboutville (in Tuxen 1970b) has compared them with those of mantids.

Internal Anatomy. Alimentary canal with a large crop extending well into abdomen; mid gut short, hind gut convoluted; 6 rectal papillae and 6 Malpighian tubules present. Nervous system concentrated with 3 discrete thoracic and 2 abdominal ganglia. Testes round or ovoid, connected to a large seminal vesicle from which runs the ejaculatory duct; a pair of accessory glands present. Female reproductive system of 4–6 panoistic ovarioles and a spermatheca, leading by a narrow tube to gonopore behind S8.

Immature Stages

The eggs are ovoid, with a finely granular chorion. Hatching is assisted by an egg-burster on the embryonic cuticle, which is shed immediately on eclosion. The nymphs are of two forms, those with wing-buds giving rise to pigmented, winged adults, and those without giving rise to pale apterous adults.

Biology

Little is known of the life histories of these gregarious insects, but there does not seem to be any social organisation. They appear to be mainly fungivorous, but mite remains have been found in the gut. Two forms of adults have been described for most species: a pigmented form, winged, with eyes and ocelli and a pale form, apterous and blind.

ACKNOWLEDGMENT. I am grateful to Dr A. B. Gurney for helpful criticism of an earlier draft of the manuscript.

Psocoptera

(*Psocids, booklice*)

C. N. SMITHERS

Small, free-living, exopterygote Neoptera, with large, mobile head, filiform antennae and bulbous postclypeus; mandibles asymmetrical; maxillae with rod-shaped lacinia; labial palps reduced; wings membranous, usually held roofwise over abdomen, venation reduced, brachyptery and aptery frequent; tarsi 2- or 3-segmented in adults, 2-segmented in nymphs; cerci absent.

Psocoptera are found in all regions. They range from less than 1 to almost 10 mm in length and have a characteristic appearance due mainly to their having a round, mobile head, long antennae, enlarged pterothorax and, in many species, the wings held roofwise over the abdomen (Fig. 28.1A). Most species are winged as adults but alary polymorphism occurs and brachyptery and aptery in one or both sexes is common. The hypopharynx is of peculiar form, modified as part of an atmospheric water-vapour uptake system (Rudolph 1982). Their relationships are not clear: their nearest living relatives appear to be the Phthiraptera but fossil evidence to link them is lacking. Psocoptera would seem to derive from primitive hemipteroid stock. Lyal (1985a) has made the interesting suggestion that the family Liposcelidae may represent the sister group to Phthiraptera in which case the Psocoptera as presently understood is a paraphyletic group. The extent to which the hypothesis rests on convergence of characters requires further investigation. The phylogenetic classification suggested by Smithers (1972) needs some modification in the light of more recent discoveries. Until these problems are resolved it is suggested that the classification currently in general use be retained for practical purposes. Publications on the order to 1964 have been listed by Smithers (1965a) and a list of described species to 1965 has been published (Smithers 1967). There are over 3000 described species. General accounts of the

order can be found in Badonnel (1951), Weidner (1972), Smithers (1972), Günther (1974) and New (1974). Study techniques are described by Smithers (1978b) and there is a key to families and genera (Smithers 1990).

Anatomy of Adult

Head (Fig. 28.1B). Large and mobile, with distinct epicranial suture; clypeus divided into narrow transverse anteclypeus and characteristically bulbous postclypeus; frons small. Compound eyes strongly convex, sometimes reduced to groups of ommatidia (e.g. *Liposcelis*); 3 ocelli present in winged forms (usually absent in apterous forms), grouped in most families on a tubercle, widely separated in some (e.g. *Lepidopsocidae*). Antennae filiform, usually 13-segmented, segments sometimes very numerous (e.g. *Lepidopsocidae*, *Trogiidae*); scape and pedicel short, remaining segments elongate. Labrum simple. Mandibles asymmetrical, with large, ridged molar area and a toothed incisor edge. Maxillae without differentiated cardo; stipes with a broad, fleshy galea strengthened by complex sclerotisations; lacinia (Fig. 28.1D) modified into an elongate, strongly sclerotised rod, proximally sunken well into head capsule, apically variously toothed; palps 4-segmented. Labium with sclerotised mentum; prementum divided; paraglossae membranous, flanking minute glossa; palps reduced, 1- or 2-segmented. Hypopharynx with extremity of lingua bearing 2 super-

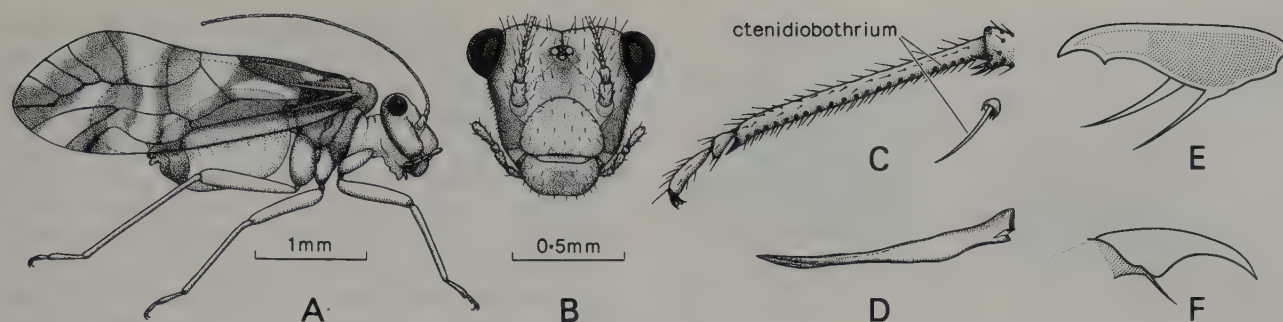


Fig. 28.1 *Pentacladus eucalypti*, Elipsocidae: A, ♂, lateral; B, head of same, anterior; C, hind tarsus and an enlarged ctenidiobothrium; D, lacinia of *Myopsocus australis*, Myopsocidae; E, claw with tooth, Elipsocidae; F, claw without tooth, Caeciliidae. [A–D by B. Rankin; E, F by T. Nolan]

linguae; lingua partially thickened ventrally into 2 oval lingual sclerites, these connected to a median sitophore sclerite by a fine filamentous duct.

Thorax. Prothorax reduced in winged forms; pterothorax well developed, the terga divided into a scutum and scutellum, behind which lies the postnotum. In apterous forms the terga of meso- and metathorax sometimes fused, without subdivision. Pleura usually developed in accordance with powers of flight, reduced in most flattened apterous forms. Sterna reduced in winged forms, broad in most flattened apterous forms. Normally 2 pairs of spiracles.

Legs. Usually slender, similar; in *Liposcelis* femora are strongly broadened. Hind coxae in many families bear on their inner surfaces a supposed stridulatory organ (*Pearman's organ*) consisting of a small rugose dome and an adjacent membranous area of integument (*tympan* or *mirror*). Trochanters without movable articulation with femur. Tibiae long, cylindrical, apically spurred, carrying *ctenidiobothria* (Fig. 28.1c); pretarsus with 2 apical claws, toothed (Fig. 28.1e) or not (Fig. 28.1f), and a variously formed pulvillus; empodia lacking.

Wings (Fig. 28.2). Membranous, hind wings smaller than fore wings, both often reduced or absent; at rest usually held roofwise over body with hind margins uppermost; coupled both in flight and at rest. Membrane usually bare, except for pterostigma; membrane occasionally hairy or with sparse setae; in some families scaled (e.g. *Lepidopsocidae*); veins and margins bare or setose. Venation of fore wing reduced; Sc reduced; pterostigma present, bounded behind by R_1 ; Rs usually 2-branched; M usually 3-branched; M fused with Rs for a length, meeting it at a point, or joined to it by a cross-vein; M and CuA fused in basal part of wing; CuA usually forked distally, the cell between the branches (*areola postica*) being a characteristic feature of the psocopteran wing (Fig. 28.3); M frequently fused with apex of areola postica, or joined to it by a cross-vein or meeting it at a point (closed discoidal cell); CuP usually finer than other veins, less often setose, runs free to margin in primitive forms, meets margin at same point (*nodulus*) as 1A in advanced forms; only one anal vein present, except in Amphientometae, some Epipsocetae and extinct families. Hind wing with venation further reduced; M and CuA usually not branched. Venational aberrations are frequent and depar-

tures from the basic plan occur in some families, either by loss (especially of CuA_1) or by additional branching. The Lower Permian Psocoptera had a more generalised venation and other primitive features.

Abdomen. Ten-segmented, terminating in a dorsal epiproct and a pair of lateral paraprocts, probably representing the 11th segment; paraprocts of winged forms usually each with a field of sensory setae (*trichobothria*). Cerci never present. Usually 8 pairs of spiracles. S9 of male (hypandrium) well developed (Fig. 28.4), delimiting an atrium genitale within which lies the phallosome which is usually simple, but sometimes ornamented with

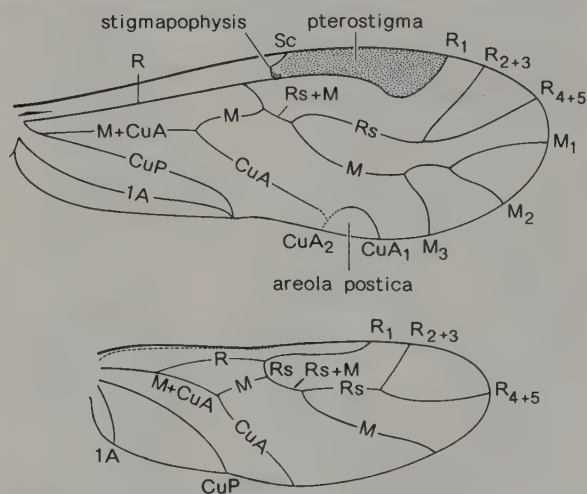


Fig. 28.2 Wing venation of *Caecilius* sp., Caeciliidae.

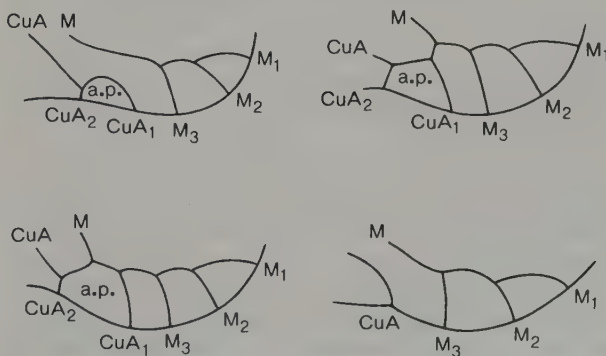


Fig. 28.3 Various relationships between M and CuA in the fore wing, with CuA dividing to form an areola postica (a.p.) or not.

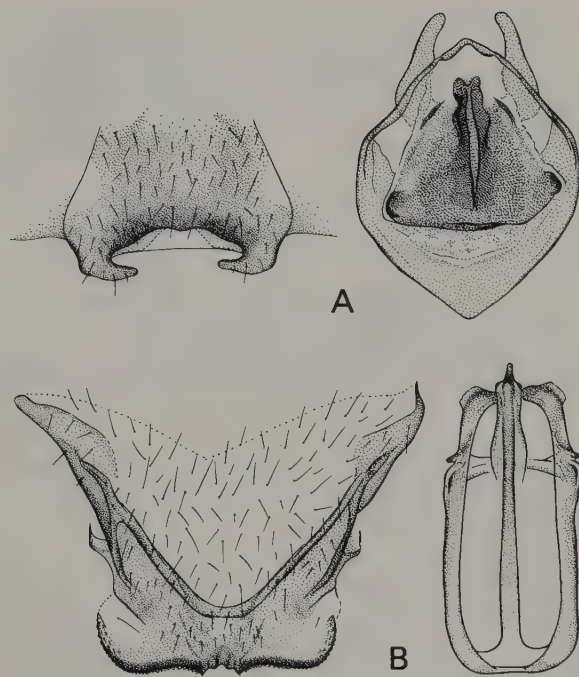


Fig. 28.4 Male hypandrium (left) and phallosome (right) of: A, *Pentacladus eucalypti*; B, *Myopsocus australis*. [B. Rankin]

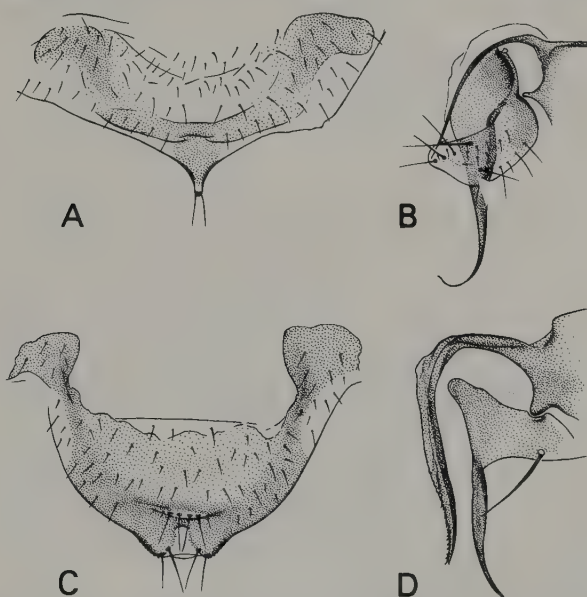


Fig. 28.5 A, subgenital plate of female *Myopsocus australis*; B, gonapophyses of same; C, subgenital plate of female *Pentacladus eucalypti*; D, gonapophyses of female *Caecilium* sp. [B. Rankin]

complex sclerotised structures (e.g. Psocidae). The phallosome consists of two 'parameres' ('external parameres' of some authors) which are sclerotised and free distally, joined basally and flank the aedeagus ('internal parameres' of some authors). Within the framework so formed lies the endophallus (penial bulb) of which the walls are frequently sclerotised in a complex manner (e.g. Peripsocidae). S7 of female forms a well-developed subgenital plate (Fig. 28.5). Ovipositor of 3 pairs of valves.

The first pair are the gonapophyses of segment 8 (ventral valves) which are usually elongate and pointed. The second and third pairs are appendages of segment 9, consisting of the dorsal valves, usually longer and broader than the ventral valves, and the external valves, short, broad and setose. Reduction of some or all of these occurs in varying degree, and they may be absent (some *Archipsocopsis* spp.). S9 frequently has some sclerotisation around the entrance to the spermatheca.

Internal Anatomy. Badonnel (1934) dealt with the internal anatomy of Psocoptera. Oesophagus elongate; mid gut wide, convoluted, leading to short hind gut; 4 Malpighian tubules. A pair of long, tubular, ventral labial glands function as salivary glands and a pair of variously formed dorsal glands as silk glands. Nervous system concentrated; meso- and metathoracic ganglia fused, a small abdominal ganglion adjacent to that of pterothorax. Two large nerves and their branches from the abdominal ganglion serve the abdomen, except for segment 1 which is served by a small pair of nerves. Testes usually 3-lobed, sometimes spherical or fusiform; vasa deferentia lead to large, complex seminal vesicles which secrete spermatophore material; ejaculatory duct short, broadening distally to form the endophallus (penial bulb) of the phallosome. Ovaries of 3–5 polytrophic ovarioles opening into common median duct via short transverse oviducts; gonopore behind S7; a spermatheca opens on S9 by a duct of variable length.

Immature Stages

The eggs are ellipsoidal, or oblong, and the chorion thin. In some families there is a thick serosal cuticle which gives the impression of a thickened chorion. Development of the embryo has been followed in only a few species. Hatching is achieved with the aid of an egg-burster on the frontal region of the embryonic cuticle, which is shed immediately after eclosion. Mockford (1987) has provided a much-needed account of nymphal stages with a key to families; although based on American species the key is useful for all areas. On hatching, the nymph is generally like the adult but always has 2-segmented tarsi, relatively short antennae, lacks ocelli and has equal thoracic segments. Meso- and metathorax become relatively larger than prothorax in later instars. There are normally 6 nymphal instars but the number may vary, especially in polymorphic species. Wing-bud development is apparent from the 2nd instar. First abdominal segment is reduced; T8–10 or 9–10 partially or completely fused, the 11th segment represented by the epiproct and paraproct. Rudiments of the external genitalia may be discernible in the final nymphal instar.

Biology

New (1987) has provided a general summary of knowledge of the biology of the order. Psocids are found on the foliage or branches of trees and shrubs, on or under bark, on fences and walls, in leaf litter, under stones, on rocks, in caves, in human habitations and in stored products.

Some species occur in several habitats but many are confined to specific vegetation types. They feed on unicellular algae, lichens, fungal hyphae, spores and fragments of plant or insect tissue. *Liposcelis bostrychophilus* has been reared on yeast media. Psocoptera are ecologically important in making the resources of the microflora available to other organisms in the food web.

Various degrees of intraspecific association are found, some species occurring in loose groups apparently brought together because of attraction to a food source or because of other environmental factors. In other cases nymphs remain in close physical contact with each other, the groups reassembling after forced dispersal of the members. The adults of such groups are usually solitary. Small groups of adults and nymphs are sometimes found under communal webs, the size of web depending on the species; in archipsocids the webs may be very extensive, covering trunks and branches of large trees. Nymphs are sometimes rendered inconspicuous by particles of debris adhering to glandular hairs; nymphs and adults may resemble their backgrounds by virtue of colour pattern.

The coxal (Pearman's) organ is presumably stridulatory in function. In one New Guinean species a presumed stridulatory apparatus involving the thorax and bases of some wing veins has been described (Smithers and Thornton 1981). The ticking noise frequently described in some domestic species is, however, caused by the underside of the apex of the abdomen being struck against the surface on which the insect is standing.

Polymorphism is fairly common in some families, the usual form involving loss or reduction of wings in the female but loss in both sexes and reduction are also known. Control of polymorphism appears to be at least in part environmental in some species. Loss or reduction of wings is frequently accompanied by loss of trichobothria, ocelli and coxal organs and retention of duplex setae on the paraprocts in adults indicating that polymorphism is associated with the phenomenon of neoteny.

Reproduction. Copulation is usually preceded by a nuptial dance, the male facing the female after which he intrudes himself backwards under her from the front. In some species the female also takes an active, even dominant, role in courtship. Courtship may last from a few minutes to ten minutes and copulation may last from a few seconds to several hours. Spermatozoa are transferred in a spermatophore which may be of complex form (e.g. in *Lepinotus*). Eggs are laid singly or in groups on or under bark, or on leaves, usually adjacent to a vein on the undersurface. They may be covered with silk or an encrustation of debris. Viviparity occurs in *Archipsocopsis* and obligatory parthenogenesis is frequent. Males are rare in some species and species are known in which males occur in some parts of their range but not others; facultative parthenogenesis also occurs.

Developmental strategy in the order varies from species to species and may vary in the same species under different environmental conditions. They may be univoltine with a period of diapause, multivoltine with diapause, facultatively multivoltine or continuously breeding.

Natural Enemies. Psocids are preyed upon by spiders,

pseudoscorpions, neuropterous larvae, ants, reduviid bugs, wasps and thrips, small birds, tree frogs and geckos. They are attacked by parasitic fungi and nematodes; the gut usually contains Protozoa. Mymarid parasites (*Alaptus*, HYMN) and cimicoid (HEMI) predators have been known to destroy eggs. Braconid wasps have been reared from nymphs and adults.

Economic Significance. Psocids are not generally of great economic importance although species associated with stored products sometimes develop enormous populations and damage to the product can result. Their occurrence is often encouraged by poor storage methods; psocids are common pests in insect collections, in libraries and in herbaria. They occasionally occur in large numbers in houses where they are a nuisance rather than destructive. It is possible that some species are intermediate hosts of tapeworms of sheep.

It should be emphasised that there is a general dearth of information on all aspects of the biology of Australian Psocoptera.

Special Features of the Australian Fauna

All families that are found in Australia are also found elsewhere. Any remarks on the faunal relationships of the Australian species must be somewhat tentative as the fauna is not yet adequately known and those of adjacent territories to the north need further study. Psocids are easily transported by air currents and have been found in samples of drifting insect populations of the upper air. Psocoptera appear to be very vagile and capable of frequently colonising new areas, establishment depending on the presence of suitable conditions and resources. Some species which are common in stored products have been widely distributed by human activity.

There are, however, certain recognisable elements in the Australian fauna. There are the cosmopolitan species, some of which are associated with people and their products, such as the many species of *Liposcelis* which are especially pests in farinaceous foodstuffs, and the species of *Lepinotus* which are found also in animal foods and on manufactured building materials such as pine-board and plywood. It is interesting that several domestic species which are common in many parts of the world have apparently not yet become established in Australia although they have been intercepted from time to time on imported materials, such as packing materials. Another group in the cosmopolitan element, including several common species of *Ectopsocus* which are associated with dried leaves and litter, appears to be naturally widespread. A second, typically Gondwanan element consists of species having relationships to those of other Southern Hemisphere areas and includes the genus *Sphaeropsocopsis*, with one species in Tas. and S.A., a species in Argentina, five species in Chile and one in Angola. A related species has been found in Baltic amber. Some of the northern Australian species represent a more or less tropical, world-encircling element (e.g. Archipsocidae) whereas others are more definitely related to Papuan forms (e.g. *Calopsocus* and *Mouldsia*). Finally, there is

the major element of the fauna consisting of species belonging to groups which are widespread beyond Australia but which have, within the Australian area, evolved many endemic species. Thornton (1985) has pro-

vided a useful review of the biogeography and ecology of arboreal species. There are only a few groups of Psocoptera the distribution of which might be related to plate tectonic events.

CLASSIFICATION

Order PSOCOPTERA (299 Australian spp.)

Suborder TROGIOMORPHA (38)

ATROPETAE (35)

1. Lepidopsocidae (25)
2. Trogiidae (9)
3. Psoquillidae (1)

PSOCATHROPETAE (3)

4. Psyllipsocidae (3)
- Prionoglarididae

Suborder TROCTOMORPHA (21)

NANOPSOCETAE (19)

5. Liposcelidae (15)
6. Pachytroctidae (3)
7. Sphaeropsocidae (1)

AMPHIENTOMETAE (2)

8. Amphientomidae (2)
- Musapsocidae
- Troctopsocidae

Manicapsocidae Compsocidae

Suborder PSOCOMORPHA (240)

EIPSOCETAE (1)

9. Epipsocidae (1)
- Cladiopsocidae
- Dolabellapsocidae
- Ptiloneuridae

CAECILIETAE (35)

10. Caeciliidae (30)
11. Stenopsocidae (1)
12. Amphipsocidae (4)
- Asiopsocidae

HOMILOPSOCIDEA (114)

13. Lachesillidae (3)
14. Ectopsocidae (25)
15. Peripsocidae (20)
16. Calopsocidae (2)
17. Pseudocaeciliidae (20)
18. Trichopsocidae (1)
19. Archipsocidae (2)
20. Elipsocidae (10)
21. Philotarsidae (30)
22. Mesopsocidae (1)

PSOCETAE (90)

23. Hemipsocidae (4)
24. Psocidae (60)
25. Psilopsocidae (1)
26. Myopsocidae (25)

The classification adopted here is that of Badonnel (1951) which is a combination of the classifications of Pearman (1936) and Roesler (1944), in both of which a range of characters was used, together with more recent modifications. Older classifications were less indicative of true relationships due partly to convergence which became more apparent when more characters were used. The suprafamily groups do not correspond to the superfamilies of other orders and it is best to regard them merely as convenient categories until the many genera requiring further study can be

reassessed. This applies especially to the Homilopsocidea. A start has been made towards bringing the nomenclature of groups of families logically more into line with that of other orders. Mockford and Garcia Aldrete (1976) have grouped the families of Caecilietae into two superfamilies, the Asiopsocoidea (to include the non-Australian Asiopsocidae) and the Caecilioidea (to include the Caeciliidae, Amphipsocidae and Stenopsocidae). Important rearrangements of the genera of the Amphipsocidae have also been made (Mockford 1978).

KEY TO THE SUBORDERS OF PSOCOPTERA—ADULTS

1. Antennae more than 20-segmented, never secondarily annulated; tarsi 3-segmented; pterostigma not thickened, or absent; paraprocts with strong posterior spine TROGIOMORPHA
- Antennae usually 13-segmented, if 12- or 15–17-segmented, some segments are secondarily annulated; tarsi 2- or 3-segmented; pterostigma thickened or not; paraprocts without strong posterior spine 2
- 2(1). Antennae 12- or 15–17-segmented, some segments secondarily annulated; tarsi 3-segmented; pterostigma not thickened TROCTOMORPHA
- Antennae usually 13-segmented; tarsi 2- or 3-segmented, if latter then flagellar segments not secondarily annulated; pterostigma thickened PSOCOMORPHA

Suborder TROGIOMORPHA

Antennae with up to 50 or more segments; filaments of hypopharynx separated for whole length; the 4 labial

glands with a common duct; female gonapophyses reduced.

Key to the Families of Trogiomorpha Known in Australia

1. Head long and vertical; maxillary palp without sensillum on 2nd segment; CuP and 1A end together at wing margin (nodulus) **Psyllipsocidae**
Head short; inner side of 2nd segment of maxillary palp with sensillum; in winged forms CuP and 1A end separately at wing margin 2
- 2(1). Claws with preapical tooth; body and wings usually scaly; if scales absent fore wings are acuminate **Lepidopsocidae**
Claws toothed; body and wings never scaly; fore wings rounded or absent 3
- 3(2). Fore wings well developed or shortened but always with veins; hind wings usually reduced **Psoquillidae**
Fore wings present only as veinless flaps, or absent; hind wings absent **Trogiidae**

1. Lepidopsocidae. Most members of this family have the body and wings scaly; in the THYLACELLINAE scales are absent but the wings are acuminate. These psocids have the appearance of small moths and are sometimes found in fairly dry situations in leaf litter and on bark. [Smithers 1965b]

2. Trogiidae (Fig. 28.6A). Several of the common indoor species of worldwide distribution belong to this family, e.g. *Lepinotus inquilinus*. They are apterous or have small, easily detached wing rudiments; the thoracic nota are not subdivided and ocelli are absent. [Smithers 1965c]

3. Psoquillidae. The widespread *Psoquilla marginepunctata*, in which the wings are dark with marginal semicircular hyaline areas, has been found in stored products in Qld.

4. Psyllipsocidae. Often pale, with long legs and capable of jumping, sometimes with reduced wings. Several representatives are found in caves and in buildings. The widespread *Psyllipsocus ramburii* is polymorphic, with brachypterous, pale, almost blind forms occurring in houses and caves and winged or brachypterous, pigmented forms with larger eyes in houses and elsewhere. Wing development appears to be affected by population density and temperature conditions.

Suborder TROCTOMORPHA

Antennae with fewer than 20 segments and with secondary annulations; filaments of hypopharynx separated only near their distal ends; female gonapophyses of various forms.

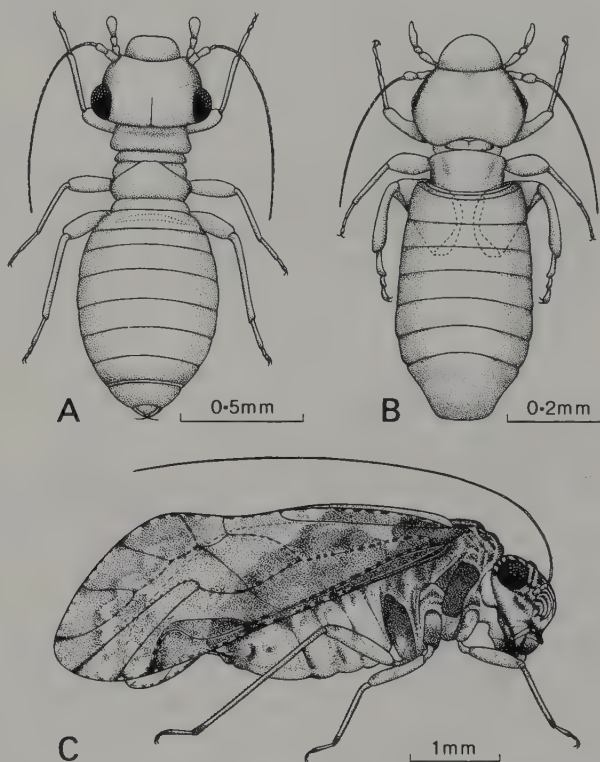


Fig. 28.6 A, *Lepinotus reticulatus*, Trogiidae; B, *Liposcelis bostrychophilus*, Liposcelidae; C, *Myopsocus australis*, Myopsocidae. [B. Rankin]

Key to the Families of Troctomorpha Known in Australia

1. Body and wings scaly **Amphientomidae**
Body and wings not scaly 2
- 2(1). Wings, when present, with complete venation. (In both alate and apterous forms eyes seated near vertex; thoracic sterna narrow, without cilia; hind femora not basally widened) **Pachytroctidae**
Wings, when present, with incomplete venation, lacking terminal branches. (In all apterous forms meso- and metathorax indistinguishably fused) 3
- 3(2). In alate forms both fore and hind wings present; eyes near vertex. In apterous forms eyes remote from vertex, each consisting of 2 large elements alone or preceded by 6 or fewer small ocelloids. Pronotum lobed; thoracic sterna broad and bearing cilia; hind femora broad basally **Liposcelidae**
In alate forms only fore wings present, convex, elytriform. In all forms eyes remote from vertex, composed of few ocelloids, none greatly enlarged; pronotum simple; thoracic sterna narrow, without cilia; hind femora not widened basally **Sphaeropsocidae**

5. Liposcelidae (Fig. 28.6B). Small, flattened species with enlarged hind femora; when wings are present, venation is reduced. Species of *Liposcelis* sometimes occur in

large numbers in stored products, houses, ships and merchandise stores; many species are of world-wide occurrence, the traditional 'booklouse' usually being one or

other species of this genus. They cause damage to insect collections and may occur in houses in sufficient numbers to be a nuisance. Members of this family are commonly found under bark.

6. Pachytroctidae. Infrequently found in or under bark or in vegetable debris. The integument of many species is sculptured.

7. Sphaeropsocidae. Small species with convex, ridged, elytriform fore wings; found in grass tussocks in Tas. and S.A. but possibly of wider distribution as this habitat

is not often investigated for psocids (Hickman 1934).

8. Amphientomidae. Two species are known from Australia (Smithers 1989).

Suborder PSOCOMORPHA

Antennae with 13 segments; no secondary annulation; filaments of hypopharynx only partly separated; female gonapophyses various. Includes the more specialised lines of development within the order and about 75% of the described species.

Key to the Families of Psocomorpha Known in Australia

1.	Adults macropterous	2
	Adults brachypterous or apterous	25
2(1).	Labrum with 2 narrow, sclerotised bands or ridges from base to distal margin	Epipsocidae
	Labrum without such bands or ridges	3
3(2).	Tarsi 3-segmented	4
	Tarsi 2-segmented	10
4(3).	Fore wings glabrous	5
	Fore wings with at least a few setae on veins and/or margin	8
5(4).	Areola postica free	7
	CuA ₁ fused with M for a length	6
6(5).	Wing pattern of dense spots and blotches	Myopsocidae
	Wing pattern of bold dark and light areas	Elipsocidae (pt)
7(5).	Areola postica shallow, extending well basal to junction of CuA ₂ and wing margin; fore wing with cloudy pattern	Psilopsocidae
	Areola postica tall, arched, not extending basal to junction of CuA ₂ and wing margin; fore wing hyaline except for pterostigma	Mesopsocidae (pt)
8(4).	Tarsal claws without preapical tooth	Pseudocaeciliidae (pt)
	Tarsal claws with preapical tooth	9
9(8).	Hind wing with marginal setae only between R ₂₊₃ and R ₄₊₅	Elipsocidae (pt)
	Hind wing with marginal setae along most of margin and posterior to R ₂₊₃	Philotarsidae (pt)
10(3).	Fore wing venation indistinct	Archipsocidae (pt)
	Fore wing venation distinct	11
11(10).	Areola postica present	13
	Areola postica absent	12
12(11).	Pterostigma more or less rectangular. Hind wing with Rs and M usually joined by a cross-vein (fused only in <i>Interpsocus</i>)	Ectopsocidae (pt)
	Pterostigma with clearly sinuous hind margin. Hind wing with Rs and M fused for a length	Peripsocidae (pt)
13(11).	Fore wing with at least a few setae on veins and/or margin	15
	Fore wings glabrous	14
14(13).	Areola postica free	Lachesillidae
	Areola postica fused with M	Psocidae (pt)
15(13).	M 2-branched in fore wing	16
	M 3-branched in fore wing	18
16(15).	Areola postica joined to M by a cross-vein	Hemipsocidae
	Areola postica free	17
17(16).	Setae of fore wing veins in a single row	Caeciliidae (pt)
	Setae of fore wing veins in a double row	Pseudocaeciliidae (pt)
18(15).	Areola postica joined to M	19
	Areola postica free	21
19(18).	Network of veins at least behind pterostigma, frequently more extensive	Calopsocidae (pt)
	No network of veins behind pterostigma	20
20(19).	Pterostigma long and narrow	Amphipsocidae
	Pterostigma with distinct widening in distal half	Psocidae (pt)
21(19).	Single row of setae on veins of fore wings	23
	Setae on veins of fore wing in two rows	22
22(21).	Network of veins behind pterostigma	Calopsocidae (pt)
	No network of veins behind pterostigma	Pseudocaeciliidae (pt)
23(21).	Cross-vein between pterostigma and Rs	Stenopsocidae
	No cross-vein between pterostigma and Rs	24
24(23).	Hind wing with apical and/or posterior marginal setae alternately longer and shorter	Trichopsocidae

	Hind wing with apical and/or posterior marginal setae all of similar length	Caeciliidae (pt)
25(2).	Tarsi 3-segmented	26
	Tarsi 2-segmented	28
26(25).	Reduced wings with at least some setae present	27
	Reduced wings with indistinct venation, glabrous	Mesopsocidae (pt)
27(26).	Setae on fore wing veins arising from dark spots	Philotarsidae (pt)
	Setae on fore wing veins not arising from dark spots	Elipsocidae (pt)
28(25).	Brachypterous	30
	Apterous	29
29(28).	Head and body with glandular setae; claws with preapical tooth	Elipsocidae (pt)
	Head and body without glandular setae; claws without preapical tooth	Archipsocidae (pt)
30(28).	Claws without preapical tooth	31
	Claws with preapical tooth	32
31(30).	Wing rudiments with discernible venation	Ectopsocidae (pt)
	Wing rudiments with venation indistinct	Archipsocidae (pt)
32(30).	Wing rudiments setose	Elipsocidae (pt)
	Wing rudiments glabrous	Peripsocidae (pt)

9. Epipsocidae. This family, a recent arrival in Australia, is represented by a single species from North Qld. Members of the family are easily recognised by the two strong bars which cross the labrum from the base to the distal margin. [Smithers 1976]

10. Caeciliidae. A large family, world-wide in distribution, with many species groups which are difficult to identify because of the great similarity of species. They are mainly inhabitants of green foliage and are usually yellow or brown, although there are dark species and some in which the wings are spectacularly marked. In the females the gonapophyses are greatly reduced to two pointed valves with a mere remnant of the external valve which usually carries a single seta (Fig. 28.5D).

11. Stenopsocidae. Like the Epipsocidae only one species of this family is now known from Australia, the *Taeniosigma* spp. previously placed in this family having been transferred to the Amphipsocidae (Mockford 1978). The Australian species is found also in New Guinea, Bali and Lombok. Stenopsocids have a strong cross-vein from pterostigma to Rs.

12. Amphipsocidae. The four species of *Taeniosigma* include some of the largest of Australia's Psocoptera. They are leaf dwellers, occurring on broad-leaved, evergreen trees, mainly in rainforests. There is a long fusion of the apex of the areola postica and M and the pterostigma is very long and narrow. [Smithers 1974]

13. Lachesillidae. Venation is of the *Caecilius* type. The wings are glabrous and the tarsi are 2-segmented; terminal structures of the male abdomen are complex but the phallosome is simple; female gonapophyses are reduced. Species of this family are found in dried leaves and in leaf litter. They have been known to occur in large numbers indoors and sometimes swarm at dusk, drifting on the wind in the manner of aphids. They are sometimes attracted to newly painted surfaces and can be a nuisance in new houses.

14. Ectopsocidae. Previously included in the Peripsocidae, ectopsocids are broad-winged species in which the wings are held relatively flatly over the abdomen. They occur in dried leaves and leaf litter, *Ectopsocus briggsi* being almost world-wide in distribu-

tion. The pterostigma is more parallel-sided than is usual in Psocoptera and there is no areola postica. The male phallosome is usually very complex and there are often additional adventitious structures on the dorsal side near the end of the abdomen. Populations of ectopsocids often reach high densities and closely related species are found living together, suggesting interesting ecological situations.

15. Peripsocidae. Essentially bark dwellers, the peripsocids also lack an areola postica; the hind margin of the pterostigma is usually sinuous. The venation of the hind wing differs from that of the ectopsocids in having Rs and M fused for a length.

16. Calopsocidae. The fore wings in this family, which is mainly tropical in distribution and has only two species in Qld, have a complex of supplementary veins behind the pterostigma, sometimes occupying much of the central area of the wings. *Calopsocus guttatus* is unusual in being brightly coloured. [Thornton and Smithers 1984]

17. Pseudocaeciliidae. Venation as in *Caecilius* but with a double row of setae on the veins. The pterostigma and areola postica are usually elongate and relatively shallow. Pseudocaeciliids are usually found on leaves or green twigs. Mockford (1984) has discussed the classification of the genera, including those from Australia. [Thornton and New 1977]

18. Trichopsocidae. Similar to the Pseudocaeciliidae, but with fewer wing setae. There is only one Australian species.

19. Archipsocidae. Wings often reduced, usually with indistinct venation, membrane setose; in viviparous species the female gonapophyses are absent, in others greatly reduced. These insects live in colonies under sheets of webbing which are sometimes so extensive as to enshroud large trees. [Smithers 1964]

20. Elipsocidae (Figs 28.1A-C). A world-wide family, with representatives living in a variety of situations. The nymphs are without glandular setae and females usually have a bilobed subgenital plate and a complete set of gonapophyses. The dorsal valve is apically divided. Most species are dull-coloured but the wings are marked with a bold pattern in *Propsocus* and *Pentacladus*. The venation

is usually of the *Caecilius* type; the hind wings have marginal setae largely restricted to the edge between R_{2+3} and R_{4+5} . [New 1972; Smithers 1963, 1964b]

21. Philotarsidae. Related to the Elipsocidae but with wings more setose, the female subgenital plate usually with a median lobe and the nymphs often with glandular setae. [Thornton and New 1977]

22. Mesopsocidae. Only one species of this family has been recorded from Australia. The hyaline wings have a tall, arched areola postica and a long, shallow pterostigma. Species of this family are predominantly grey and are often found in dry environments, mainly on shrubs.

23. Hemipsocidae. Distinguishable by 2-branched M and areola postica connected to M by a cross-vein. Many species have conspicuous spots on the fore wings from which the setae arise. They are active when disturbed, fluttering and tumbling in a characteristic manner. They are mainly inhabitants of leaf litter and dried leaves.

24. Psocidae. A large family of bark-dwelling species in which the areola postica is joined to M for a length; the fore wings are nearly always glabrous. They are sombre-

coloured species exhibiting a wide range of genitalic features.

25. Psilopsocidae. The only species of this small family to occur in Australia has been found near Sydney, where it is not often encountered. The nymphs are peculiar in that the apex of the abdomen is strongly sclerotised with the epiproct and paraprocts in a ventral position forming a cover to the anus. They are probably inhabitants of the burrows of beetle larvae. [Smithers 1983a]

26. Myopsocidae (Fig. 28.6). Large, common, mottled-winged species, found on paling fences and on bark, where they feed on algae and lichens. [Smithers 1964c, 1975]

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Phthiraptera

(Lice)

J. H. CALABY and M. D. MURRAY

Apterous, dorsoventrally flattened, exopterygote Neoptera, with mouth-parts mandibulate or piercing and sucking. Ectoparasitic on birds and mammals; entire life spent on hosts.

This highly specialised order was undoubtedly derived from free-living psocopteroid ancestors. It is divided into four very distinct suborders, the Amblycera and Ischnocera (chewing or biting lice, previously grouped together as the Mallophaga), Rhyncophthirina (elephant lice, also previously included in Mallophaga by some authors) and Anoplura (sucking lice). Over 3000 species are known. There is a great diversity in size and body form (Figs 29.1, 4). The adults range in length from less than 0.5 to 10 mm (males are usually smaller than females). They are highly modified for their parasitic existence, the most characteristic features being flattening of the body, complete aptery, and adaptations of tarsi for clinging to the feathers or hair of the host. Most species are well sclerotised, many are deeply pigmented, and some have a characteristic pattern. In some groups the body is covered with setae, but in others it is relatively bare.

The Rhyncophthirina are an anomalous group, which includes only the genus *Haematomyzus* parasitising African and Asian elephants and the African wart-hog; they are not considered in this chapter. General literature on the other suborders includes Hopkins and Clay (1952), Rothschild and Clay (1952) and Blagoveschenskii (1959) on Amblycera and Ischnocera, Hopkins (1949) on Amblycera, Ischnocera and Anoplura of mammals, and Ferris (1951), Kim and Ludwig (1978a) and Kim *et al.* (1986) on Anoplura.

Anatomy of Adult

Head. Sessile or with limited movement in the vertical axis on prothorax, long axis in same plane as rest of body; in Amblycera and Ischnocera generally compressed dorsoventrally, with sutures and thickened internal apodemes, both of which provide useful generic characters. Eyes reduced or absent; ocelli absent. Antennae 3–5-segmented; in Amblycera usually capitate and lying in a groove; in Ischnocera and Anoplura filiform, exerted, and sometimes modified in the male as clasping organs. Mouth-parts mandibulate in Amblycera and Ischnocera (Fig. 29.2A), and differ in their insertion in the two suborders; maxillary palps 2–4-segmented in Amblycera, absent in Ischnocera. In Anoplura anterior part of head is an unjointed, more or less conical or rounded beak (Fig. 29.2C); the mouth-parts consist of a small soft proboscis (haustellum) with small internal teeth, which is eversible to grip the host during feeding, and 3 stylets, the piercing organs, accommodated in the stylet (trophic) sac opening off the ventral side of the cibarium; maxillary palps absent.

Thorax. Prothorax almost always free, meso- and metathorax often imperfectly separated in Amblycera and Ischnocera; all segments fused in Anoplura.

Legs. Well developed, especially stout in the Anoplura. In Amblycera and Ischnocera tarsus 1- or 2-segmented, bearing a pair of claws in most families, but single claws

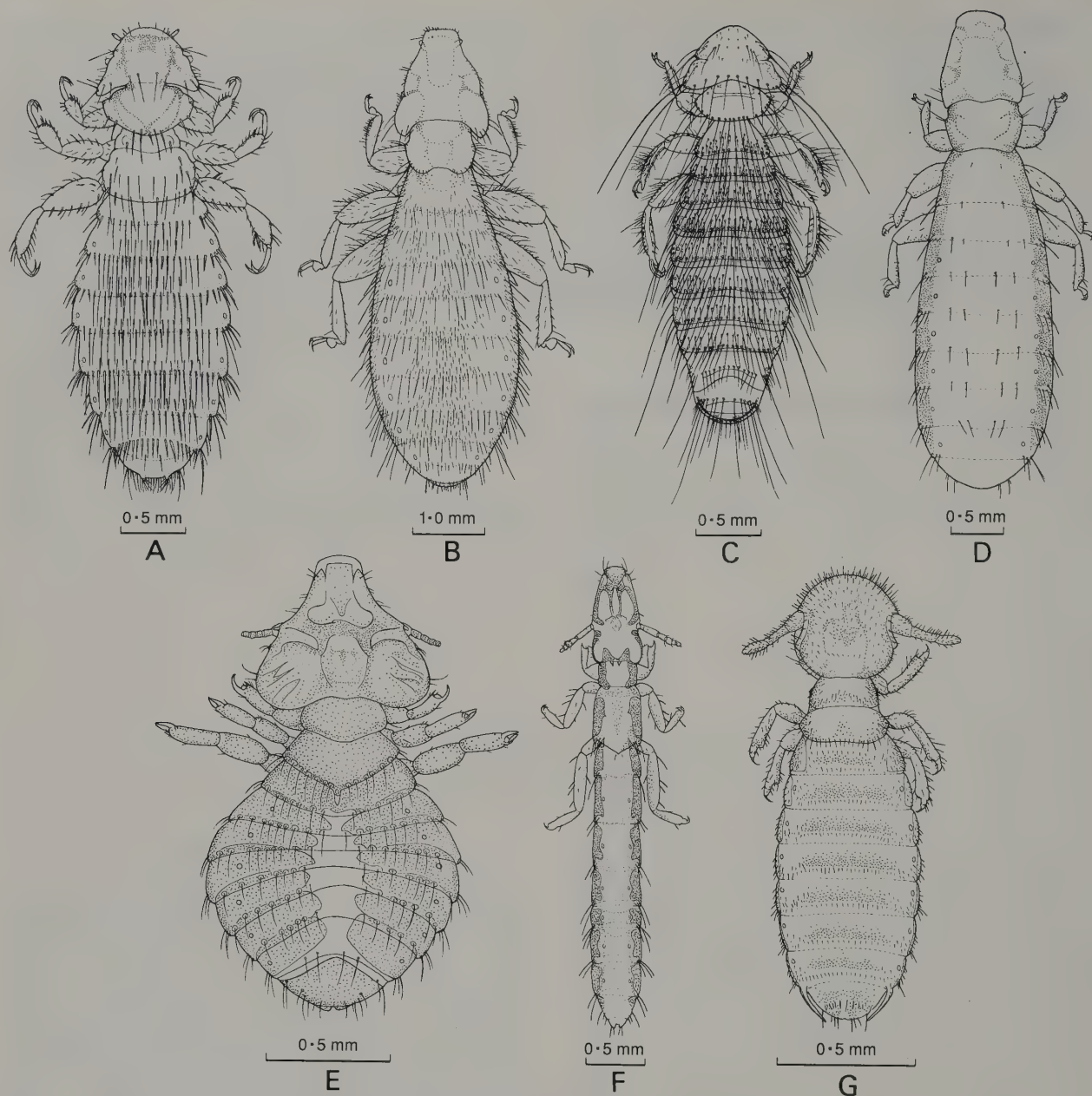


Fig. 29.1 Representative Amblycera and Ischnocera: A, *Paraheterodoxus insignis*, Amblycera-Boopidae, ♀ from *Aepyprymnus rufescens*; B, *Laemobothrion tinnunculi*, Amblycera-Laemobothriidae, ♂ from *Falco cenchroides*; C, *Menacanthus stramineus*, Amblycera-Menoponidae, ♂ from *Gallus gallus*; D, *Ricinus ernstlangi*, Amblycera-Ricinidae, ♀ from *Turdus merula* (exotic); E, *Saemundssonina platygaster*, Ischnocera-Philopteridae, ♀ from *Charadrius bicinctus*; F, *Halipeurus diversus*, Ischnocera-Philopteridae, ♀ from *Puffinus tenuirostris*; G, *Bovicola ovis*, Ischnocera-Trichodectidae, ♀ from *Ovis aries*. [F. Knight]

in three mammal-infesting families; in Anoplura tarsus 1-segmented or weakly 2-segmented, with single large claw working against a tibial process (Fig. 29.2b).

Abdomen. Number of visible segments varies from 8 to 10, 9 in the Anoplura. Cerci absent. Penis of male has a permanently-everted endophallus; anatomy of male genitalia (Fig. 29.2g) important in taxonomy. Ovipositor absent, but there is a pair of short 'gonopods' (gonapophyses 8) in Anoplura (Fig. 29.2b) and some Amblycera and Ischnocera which are concerned with grasping the hair of the host and placing eggs on it. In females of many species the last segment terminates in 2 posterior lobes or

claspers. Lyal (1986) has carried out a detailed study of the genitalia.

Internal Anatomy. In Amblycera and Ischnocera there is a well-developed crop and a large mid gut; hind gut usually short, but may be almost as long as mid gut. In Anoplura crop and proventriculus undeveloped, and mid gut large; cibarium and pharynx and their dilator muscles form powerful sucking pump. There are 4 Malpighian tubules and 4 or more, usually 6, rectal glands. Tracheal system of Amblycera and Ischnocera, to which that of Anoplura is generally similar, has been studied by Harrison (1915). The female reproductive system

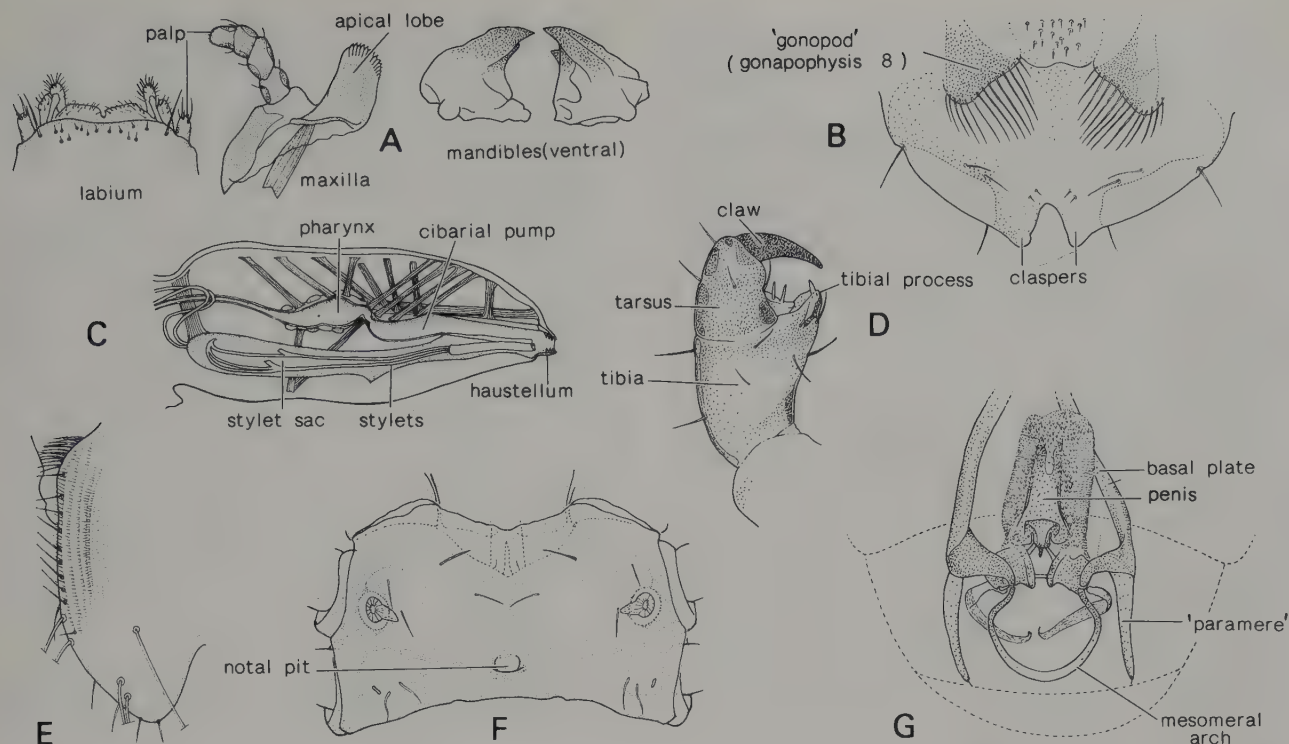


Fig. 29.2 A, mouth-parts of *Laemobothrion* sp., Amblycera-Laemobothriidae (after Snodgrass, 1905); B, ♀ terminalia of *Haematopinus asini*, Anoplura-Haematopinidae; C, median sagittal section of head of *Pediculus humanus*, Anoplura-Pediculidae (after Buxton 1947); D, fore leg of *Haematopinus asini*; E, side of head of *Laemobothrion* sp., showing rows of minute projections posterior to eye; F, thoracic nota of *Haematopinus asini*, showing notal pit; G, ♂ genitalia of *Paraheterodoxus insignis*, Amblycera-Boopidae. [F. Knight]

includes an accessory gland to provide cement for egg attachment.

Immature Stages

The eggs (Fig. 29.3) are elongate oval, commonly whitish; in some species ornamented with surface sculpturing or plume-like processes associated with the operculum; large relative to size of host, varying from less than 1 to nearly 2 mm in length. Nymphs resemble the adult generally, but are much smaller and unpigmented in 1st instar, becoming successively larger and darker after each ecdysis.

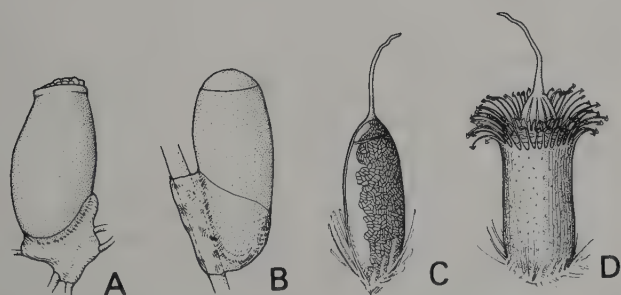


Fig. 29.3 Eggs of Phthiraptera: A, *Pediculus humanus*, Anoplura-Pediculidae, from *Homo sapiens* (after Ferris 1951); B, *Haematopinus suis*, Anoplura-Haematopinidae, from *Sus scrofa* (after Ferris 1951); C, *Brueelia* sp., Ischnocera-Philopteridae, from a passerine bird (after Richter, in Balter 1968); D, *Kelerimenopon* sp., Amblycera-Menoponidae, from an Australian megapode (after Richter, in Balter 1968). [F. Knight]

Biology

Adults. All orders of birds are parasitised and most orders of mammals, and the degree of host specificity is generally high (Hopkins 1949). Because of their host specificity, and the fact that most genera of lice parasitise related hosts, the louse fauna may provide important clues where host relationship is in doubt. Taxonomic studies, including electrophoretic, on relationships of lice of the *Heterodoxus octoseriatus* and *H. ampullatus* complexes have contributed to an understanding of the evolution of rock-wallabies (*Petrogale*) (Clay 1981; S. C. Barker 1986). The higher classification of birds is unsatisfactory, owing, at least in part, to their apparently rapid evolution and lack of fossils. The lice presumably became established on birds early in their history, and louse evolution has been more conservative than that of their hosts. For example, the flamingoes are usually placed with the storks and herons (Ciconiiformes), but occasionally with the swans, geese and ducks (Anseriformes), and it may be significant that they share with the Anseriformes 3 genera of lice not found on the Ciconiiformes. This kind of evidence is not necessarily convincing, however, because the louse fauna of a host species may have been acquired secondarily from another host at some time during its history. On the other hand, Lyal (1985a) concluded that 'there is no evidence to suggest that lice were present on any but the Recent orders of mammals and birds . . .'. The number of species present on a host species varies from as low

as one up to 15 in 12 genera and 3 families on a South American tinamid (Clay 1949). There are generally 2–6 species of lice per host species of bird and 1–3 per mammal species.

In general, lice occupy specific regions on their hosts' bodies, those of mammals probably being less restricted than those of birds. A bizarre example is the amblyceran genus *Piagetiella*, the species of which feed on the interior lining of the bill pouches of pelicans and a few species of cormorants. *P. australis* on *Pelecanus conspicillatus* is an Australian representative. Well-known examples of specific niches are also provided by the human lice and the lice of sheep.

In general, Ischnocera of birds feed on feathers (usually the downy parts) and those of mammals on the surface of the skin. Amblyceran lice may feed on feathers, skin surface or blood. The common fowl louse *Menacanthus stramineus* habitually punctures developing quills to obtain blood, and also bites through the skin. *Heterodoxus* spp. of wallabies feed on blood. Some Amblycera also feed on eggs and nymphs of other lice (B. C. Nelson 1971). The Anoplura feed exclusively on blood. The feathers of birds and the pelage of mammals is frequently an arid habitat. Many Amblycera and Ischnocera can obtain moisture from the air (Rudolph 1983).

Amblycera and Ischnocera are generally more active than Anoplura. Lice are negatively phototropic, and the numerous sensory setae no doubt help to guide them through the feathers or hair. The antennae are important sensory organs. Lice are sensitive to the temperature and smell of their hosts. Optimum temperatures for feeding and reproduction are just below that of the skin surface, and close to the upper limits of thermal tolerance. The insulating properties of the feathers or hair ensure that the habitat is relatively uniform in temperature and humidity gradients. As the temperature of a dying host decreases, these gradients are destroyed and the lice are found on the outside of plumage or pelage, and their movements become very slow. They usually survive for only a few days off the host.

Transfer between individual hosts is principally by contact: during brooding or nursing of young, during copulation, at roosts or communal sleeping places of gregarious species, or in common dust baths. Accidental transfers take place from prey to predator, and probably some species of genera which are common to predator and possible prey species originally arose on the predator by such means. Phoresy—the transport of Ischnocera by other insects, particularly hippoboscids and muscid flies—has been reported.

The number of lice present on individual hosts varies from nil to many thousands. In general, small hosts have few—small birds usually fewer than 10—and large hosts have larger numbers. Some figures for mammals are given by Hopkins (1949), who found that in a number of species nymphs were roughly twice as numerous as adults. Little is known of the longevity of adult lice. There is some evidence that females live longer than males. The average adult life of the two species infesting man is about a month. The maximum life of the female of

Bovicola bovis has been given as 42 days (Matthysse 1944). The maximum adult lives of males and females of *Haematopinus eurysternus* are 10 and 16 days (Roberts 1952). Some individuals of the highly specialised *Lepidophthirus macrorhini* can survive the several months while its host, the elephant seal, is at sea (M. D. Murray and Nicholls 1965).

In natural populations of lice females are usually in excess, and in some species males may be very rare (see Hopkins 1949); Matthysse (1944) has shown that *B. bovis* is facultatively parthenogenetic, and that males are most numerous in rapidly increasing populations. A few species are entirely parthenogenetic. Pairing occurs frequently in *Pediculus humanus*, and one male may fertilise many females (Buxton 1947). Lice usually lay their eggs in favoured sites, cemented to the feathers or hairs (Fig. 3.23). Common egg-laying sites on birds are along the grooves between the barbs of flight feathers close to the shaft and in the downy feathers of the body close to the skin. In these sites they escape the bill of the preening bird. On mammals they are usually attached to a hair close to the skin.

Oviposition behaviour of mammalian lice, the distribution of eggs, and influence of environmental factors have been studied by M. D. Murray (1957a–d, 1960a, b). In experimental situations a *Bovicola ovis* female moved to the warm end of a temperature gradient some time before laying eggs. Here it rested with its head towards the warm end while abdominal contractions took place. About five minutes before egg-laying, the louse suddenly turned around so that the abdomen pointed in the direction of the warmest temperature. The gonopods were raised, and moved around until the wool fibre was caught and held against the abdomen. After a few seconds, cement was secreted, then all of the egg except the cap was expelled. After a short time the louse walked along the fibre, thus assisting the expulsion of the cap end of the egg. The oviposition behaviour of other species was broadly similar. In some species the gonopods are also used as moulds for the cement, and hence attachments may be characteristic for a species.

Egg-laying was inhibited by the absence of suitable fibres and very high humidities, but the presence of light had no effect. Eggs are laid within a narrow temperature range, and in *Linognathus pedalis* development of the eggs was completed only within a narrow range. Very high humidities also caused hatching failure. The distribution of eggs on the body of the host is determined by the optimum temperature zone, which is regulated by skin temperature, skin topography, thickness of air blanket trapped in the pelage, and the ambient temperature.

The number of eggs laid daily or in a lifetime varies with the species. *P. humanus* may lay as many as 300 but *Bovicola bovis* only up to 30. The number of eggs laid daily may be as few as 1 every 2–3 days for *Columbicola columbae* (M. Martin 1934) or as many as 10 per day for *P. humanus*.

Eggs take 5–18 days to develop and hatch depending on species. Hatching behaviour has been described for a few species, e.g. *C. columbae* by M. Martin (1934) and

Polyplax serrata by Sikes and Wigglesworth (1931). When the pharate nymph is ready to hatch, air is sucked through the mouth to accumulate in the gut. The resultant pressure from this air and that which has already accumulated inside the shell behind the nymph becomes so intense that the operculum is forced open, and the nymph frees itself during the next 20 minutes by muscular contractions, abdominal expansion, and further sucking of air. *P. humanus* and some other Anoplura have hatching devices, a pair of upcurved teeth and several pairs of blades, on a rigid area of embryonic cuticle on the front of the head. At the appropriate time, the blades probably pierce the vitelline membrane, and the teeth force up the cap of the egg. The length of the life cycle can vary from 13–43 days depending on the species, and some representative figures are given in Table 29.1. These variations in daily egg production and generation times lead to considerable differences in their reproductive potentials, indicating major differences in their ecology (M. D. Murray 1987a).

Natural Enemies. The principal enemies of lice are their hosts, and the importance of population control by preening and grooming has been demonstrated experimentally. Dust-bathing in birds probably helps to rid them of their lice, and the habit may have evolved as a response to ectoparasitic irritation. The curious phenomenon of 'anting' in birds may also be a response to louse irritation. Fragments of lice have been found in the gut of other lice.

Economic Significance. Anoplura are known to transmit the organisms responsible for several diseases of humans and other animals. The most important is epidemic typhus in humans, transmitted by *P. humanus*. This infection has fortunately been absent from Australia since the early days of settlement. Murine typhus may be transmitted among rats by *Polyplax spinulosa*, but the principal vector is a flea. Other blood parasites may be transmitted by lice. The virus of rabbit myxomatosis can

be transmitted mechanically by the rabbit louse, *Haemodipsus ventricosus*. *Trichodectes canis* may serve as an intermediate host of the dog tapeworm *Dipylidium caninum*. Heavy infestations with lice cause considerable production losses in the wool, meat, dairying and poultry industries, and blood-sucking species may even kill very young animals. The veterinary importance of lice in Australia has been discussed by Roberts (1952).

Special Features of the Australian Fauna

The Phthiraptera are among the least known of Australian insects. From a consideration of the bird and mammal fauna, a conservative estimate of the louse fauna would be 2500 species, yet only about 200 native species have been recorded. Reasons for this are that the collection of the lice involves the tedious examination of dead or captured vertebrate hosts, and there are few taxonomists competent in this group.

As in other zoogeographical regions, the great majority of bird lice belong to the large families Menoponidae and Philopteridae. The other bird-infesting families are small and parasitise a limited range of hosts. As single genera of lice usually parasitise one or more host orders, it is not surprising that the only endemic genera so far discovered occur on the emu and on marsupials. The family Boopiidae is almost restricted to Australian and Papuan marsupials and contains most of the amblyceran lice found on mammals. There are only a few native species of Anoplura, as the only available hosts are rodents and seals. It is of interest that lice have not been found on monotremes or some families of marsupials—koala, possums, gliders, pigmy possums, honey possum, numbat, marsupial mole. Lice are not found on bats.

The Australian louse fauna may be divided into four categories: (1) endemic species from endemic host species (the great majority); (2) widespread species occurring on hosts that occur also in other parts of the world (e.g. *Tyto alba* and many species of sea birds, par-

Table 29.1 Average life cycles of some species of mammalian lice under optimal conditions

Stage (days)	<i>Pediculus humanus</i> (Buxton 1947)	<i>Polyplax serrata</i> (Murray 1961)	<i>Haematopinus eurysternus</i> (Roberts 1952)	<i>Linognathus pedalis</i> (Scott 1950; minima)	<i>Bovicola ovis</i> (Scott 1952)
Incubation	9	6	12	17	9–10
1st instar)			4	7	7
2nd instar)	9	7	4	7	5
3rd instar)			4	7	9
Pre-oviposition	2		4	5	3
Egg to egg	20	13	28	43	34
Host	Human	Mouse	Cattle	Sheep	Sheep
No. of eggs laid daily	9	2	4	1	0.4

ticularly petrels); (3) species which are apparently not very host specific and occur on native hosts, but which are not specifically distinguishable from lice occurring on related hosts in other parts of the world (e.g. *Saemundsonia africana* on *Vanellus miles* is only subspecifically distinct from the louse on a related African plover; a louse

found on *Corvus tasmanicus* in Tas. is indistinguishable from *Colpocephalum fregili* found on a European corvid, *Pyrrhocorax pyrrhocorax*); (4) introduced species parasitising domestic and feral introduced birds and mammals, including humans, among which are most of the Anoplura.

CLASSIFICATION

Order PHTHIRAPTERA

(255 Australian spp.)

Suborder AMBLYCERA (107)

- | | | |
|--------------------|------------------------|---------------------|
| 1. Boopiidae (49) | 2. Gyropidae (2) | 4. Menoponidae (50) |
| Trimenoponidae (0) | 3. Laemobothriidae (4) | 5. Ricinidae (2) |

Suborder ISCHNOCERA (123)

- | | | |
|------------------------|-----------------------|-----------------------|
| 6. Philopteridae (117) | Heptasogasteridae (0) | 7. Trichodectidae (6) |
|------------------------|-----------------------|-----------------------|

Suborder RHYNCOPHTHIRINA (0)

Haematomyzidae (0)

Suborder ANOPLURA (25)

- | | | |
|--------------------------|------------------------|----------------------|
| 8. Echinophthiriidae (2) | 10. Hoplopleuridae (7) | 13. Polyplacidae (3) |
| 9. Haematopinidae (5) | 11. Linognathidae (6) | 14. Pthiridae (1) |
| | 12. Pediculidae (1) | |

The families of Amblycera and Ischnocera are those recognised by Hopkins and Clay (1952), and of Anoplura those in Kim *et al.* (1986). There is no agreement among authors on the classification of lice, not even on whether they should be included in one or two orders. In particular there is disagreement over whether the suborder name Mallophaga should be dropped. Clay (1970), Haub (1980)

and Lyal (1985a) argue for there being four suborders—Amblycera, Ischnocera, Rhyncophthirina and Anoplura and give many sound phylogenetic reasons. On biological grounds the Amblycera and Ischnocera are certainly very different. Kim and Ludwig (1978b, 1982) argue for the retention of Mallophaga. The classification given here has been chosen for simplicity of identification.

Key to the Suborders and Families of Phthiraptera Known in Australia

(couplets 9–14 based on Kim *et al.* 1986)

1. Head relatively small (Fig. 29.4); mouth-parts developed into an unjointed more or less pointed beak, or rounded anteriorly, without mandibles; on mammals ANOPLURA. 9
- 2(1). Head relatively large (Fig. 29.1); mouth-parts mandibulate; on birds and mammals 3
- 3(2). Antennae concealed in grooves (Figs 29.1A–D), generally capitate, usually 4-segmented, 3rd segment wineglass-shaped; mandibles horizontal; maxillary palps 2–4-segmented; meso- and metathorax usually separate AMBLYCERA. 4
- Antennae not concealed (Figs 29.1E–G), usually filiform, 3–5-segmented; mandibles vertical; maxillary palps absent; meso- and metathorax usually fused ISCHNOCERA. 8
- 4(3). Tarsi single-clawed; in Australia only on captive guinea-pigs Gyropidae
- Tarsi with paired claws; on birds, marsupials, canids 5
- 5(4). Mesonotum with 2 protuberances, each bearing a spine-like seta (Fig. 29.1A); spiracles on apparent abdominal segments 2–7; apparent abdominal terga 1–3 with a fine trichobothrium on each side, or, if these are absent, maxillary palps with less than 4 segments Boopiidae
- Without this combination of characters 6
- 6(5). Abdominal segment 1 fused to thorax; spiracles on apparent segments 2–7. [Head elongate (in *Ricinus*, Fig. 29.1D); base of antenna widely removed posteriorly from base of maxillary palp] Ricinidae
- Without this combination of characters 7
- 7(6). Head elongate (Fig. 29.1B), with strong swelling of lateral margins in front of eye, followed by approximately parallel lateral margins to horizontal (flattened or concave) anterior margin; base of antenna widely removed posteriorly from base of maxillary palp; lateral area posterior to eye with rows of minute projections (Fig. 29.2E); hind femur and some sternites with dense patches of microtrichia Laemobothriidae
- Without this combination of characters Menoponidae
- 8(3). Antennae 3-segmented (Fig. 29.1G); tarsi single-clawed; on introduced mammals Trichodectidae
- Antennae 5-segmented (Figs 29.1E, F); tarsi with paired claws; on birds Philopteridae

- 9(1). Head with distinct eyes or ocular points behind antennae 10
 Head without eyes or ocular points 12
- 10(9). Head with eyes having distinct lens but without ocular points; on humans 11
 Head with prominent ocular points but without eyes with lens; on ungulates **Haematopinidae**
- 11(10). Abdomen much longer than basal width, without hairy lateral tubercles; all three pairs of legs subequal
 **Pediculidae**
 Abdomen compact, about as long as basal width, with hairy lateral tubercles; fore legs smaller and more slender than mid and hind legs **Pthiridae**
- 12(9). Head and thorax covered with setae, abdomen thickly covered with various setae including scales and spines; on seals
 **Echinophthiriidae**
 Head and thorax with only a few typical setae, abdomen without scales; on land mammals 13
- 13(12). Abdomen with distinct paratergites; fore coxae usually close together; on rodents and lagomorphs 14
 Abdomen without distinct paratergites; fore coxae widely separated from each other; on ungulates and carnivores
 **Linognathidae**
- 14(13). S2 extending laterally on each side to articulate with the corresponding paratergites; hind legs largest of the 3 pairs; on rodents **Hoplopleuridae**
 S2 narrow, not extending laterally; mid legs subequal in size to hind legs; on rodents and lagomorphs ... **Polyplacidae**

Suborder AMBLYCERA

1. Boopidae (Fig. 29.1A). With two exceptions this family of 7 genera and over 50 species is confined to Australian and Papuan marsupials. A revision by von Kéler (1971), based on material collected from wild-caught hosts, recognised 35 species. Since then another 17 species have been described and several others await description. Only one-third of the currently-recognised families of Australasian marsupials are known to be parasitised, including the two largest ones; Dasyuridae (marsupial-mice, native cats, etc.) and Macropodidae (kangaroos). One 'non-marsupial' boopiid is *Heterodoxus spiniger*, which occurs on domestic dogs in many parts of Australia, Africa, Asia and the Americas, and has been found also on *Macropus agilis*. It is probable that *H. spiniger* transferred to dogs, perhaps via the dingo, and was transported around the world on domestic dogs. There are reliable records of *H. spiniger* from the jackal and coyote. *Therodoxus*, closely related to *Heterodoxus*, was described from New Guinea from the cassowary, *Casuarius casuarius*, which also occurs in Australia. The ancestor of *Therodoxus* possibly established on these large ground birds from some species of wallabies which live in the same forest habitat (Clay 1971).

One genus of another South American family of Amblycera, the Trimenoponidae, is parasitic on marsupials, both didelphids and caenolestids. This family is not closely related to the Boopidae and almost certainly had different origins.

2. Gyropidae. Two species (*Gyropus ovalis* and *Gliricola porcelli*) of this South American family have been recorded in Australia on captive guinea-pigs, their natural host.

3. Laemobothriidae (Fig. 29.1B). The only included genus, *Laemobothrion*, is parasitic on rails, storks and hawks. Three of the four valid species of *Laemobothrion* (*Laemobothrion*), a subgenus restricted to the Falconiformes, are cosmopolitan and occur on Australian hosts. The species present on the coot (*Fulica atra*) appears to be *L. atrum* which occurs on the same host in Europe.

4. Menoponidae (Fig. 29.1C). This family, much the largest of the suborder, is world-wide in distribution, and

occurs on all orders of birds that have been studied sufficiently. Approximately 40 native species in about 20 genera have been recorded from Australian birds. Roberts (1952) lists those recorded from poultry and the domestic pigeon, among the more important being *Menacanthus stramineus* and *Menopon gallinae* on fowls and *Colpocephalum turbinatum* on pigeons.

5. Ricinidae (Fig. 29.1D). This family consists of 2 genera, one on Neotropical humming-birds and the other (*Ricinus*) parasitising small passerines of many families. *Ricinus* is found on several passerine families in Tas. and south-eastern Australia. These lice seem incongruously large relative to the size of their hosts.

Suborder ISCHNOCERA

6. Philopteridae (Figs 29.1E, F). This is the largest family of lice, and contains numerous genera and species found on all orders of birds in all parts of the world. About 100 native species in about 45 genera have been recorded from Australia, including the one endemic genus of the family (*Dahlehornia* from the emu, *Dromaius novaehollandiae*). Several introduced species have been recorded from domestic poultry and introduced feral birds. Roberts (1952) lists those from domestic poultry and the pigeon, among the more important being *Lipeurus caponis*, *Cuclotogaster heterographus*, *Goniodes dissimilis* and *Goniocotes gallinae* on fowls, and *Anatoecus dentatus* and *Anaticola crassicornis* on ducks. *Columbicola columbae* is common on the domestic pigeon.

7. Trichodectidae (Fig. 29.1G). A family of 20 genera (Lyal 1985b) and many species parasitising a great variety of mammals in most parts of the world. Several have been introduced into Australia with their domestic hosts: *Bovicola bovis* (cattle), *B. ovis* (sheep), *B. caprae* (goat), *Werneckiella equi* (horse), *Trichodectes canis* (dog, including the dingo), *Felicola subrostratus* (cat).

Suborder ANOPLURA

8. Echinophthiriidae. There are 5 genera in this family; 4 are found on seals and the other on the river otter *Lutra canadensis* in North America. In Australia lice have

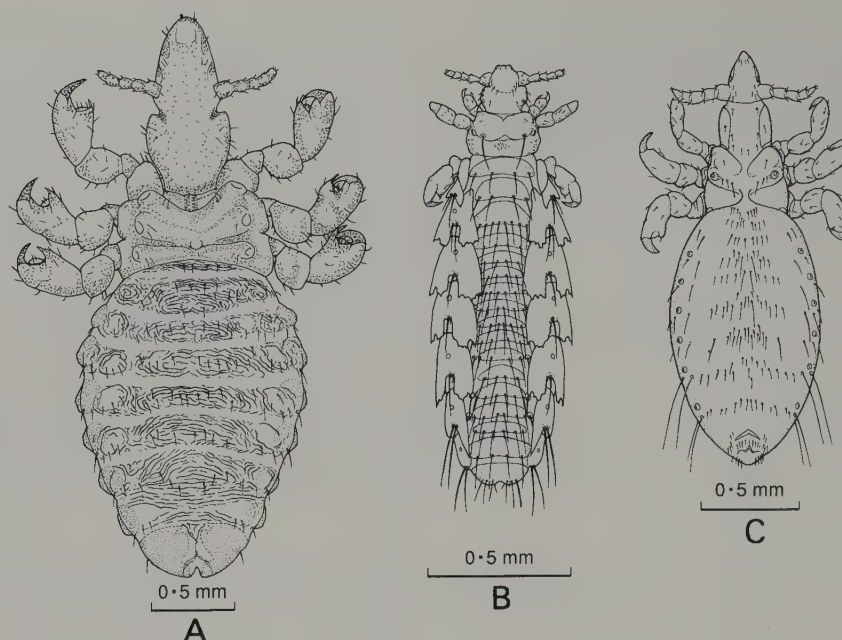


Fig. 29.4 Representative Anoplura: A, *Haematopinus asini*, Haematopinidae, ♀ from *Equus caballus*; B, *Hoplopleura calabyi*, Hoplopleuridae, ♀ from *Pseudomys higginsii*; C, *Linognathus vituli*, Linognathidae, ♂ from *Bos taurus*. [F. Knight]

been found on the fur seal (*Arctocephalus*), the sea lion (*Neophoca*) and vagrant leopard seals (*Hydrurga*).

9. Haematopinidae (Fig. 29.4A). The species in this family are best known as parasites of ungulates, and those present in Australia are important pests of domestic stock: *Haematopinus eurysternus* and *H. quadripertusus* on cattle, *H. suis* on pigs, and *H. asini* on horses. *H. tuberculatus* is common on buffalo (*Bubalus bubalis*) in northern Australia, and is occasionally found on cattle.

10. Hoplopleuridae (Fig. 29.4B). The family contains many genera, and the chief hosts are rodents. *Hoplopleura* contains the only native Anoplura, and there must be many more species than the few described. *H. pacifica*, a common parasite on *Rattus rattus* and *R. exulans* in the Pacific, is common on *R. rattus* in Australia.

11. Linognathidae (Fig. 29.4C). *Linognathus* parasitises ruminants and canids, and the species present in Australia are all parasites of domestic mammals: *L. pedalis* and *L. ovillus* on sheep, *L. vituli* on cattle, *L. stenopsis* on goats and *L. setosus* on dogs, including the dingo. *Solenopotes capillatus* occurs on cattle.

12. Pediculidae (Fig. 3.25D). This family is parasitic on primates. *Pediculus* occurs on humans and other hominoids and on Neotropical monkeys. The human head (*P. capitus*) and body (*P. humanus*) lice are sibling species.

13. Polyplacidae. In Australia, one genus occurs on introduced lagomorphs and, although the rabbit louse *Haemodipsus ventricosus* is common, the hare louse *H. lyriocephalus* has not been recorded. Species of *Polyplax* infest introduced species of rats and mice, and *P. spinulosa*, which is common on *Rattus rattus* and *R. norvegicus*, is also found on some native species of *Rattus* in settled areas.

14. Pthiridae. The only species present is the human crab louse *Pthirus pubis*.

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Hemiptera

(*Bugs, leafhoppers, cicadas, aphids, scale insects etc.*)

M. CARVER, G. F. GROSS and T. E. WOODWARD

With contributions by G. Cassis, J. W. Evans, M. J. Fletcher, L. Hill, I. Lansbury, M. B. Malipatil, G. B. Monteith, M. S. Moulds, J. T. Polhemus, J. A. Slater, P. Štys, K. L. Taylor, T. A. Weir and D. J. Williams

Exopterygote Neoptera which feed by suction, the mouth-parts consisting of hinged stylets—mandibles and maxillae—resting in an anteriorly grooved rostrate labium; suction canal and salivary canal both lying between the maxillary stylets; maxillary and labial palps absent; usually two pairs of wings, the fore wings may be entirely or in part of harder consistency than the hind wings; cerci reduced or absent. Metamorphosis usually gradual.

The Hemiptera are the dominant group of exopterygote insects. They range in length from less than 1 to 110 mm, and comprise insects with a great range of different structural and behavioural features and occupying a wide variety of environments. The most characteristic feature is the structure of the mouth-parts, which are highly efficient for extracting the liquid contents of plants or of animal prey. The basic structure of the mouth-parts has remained unaltered throughout the Hemiptera, and is diagnostic of the order. Most Hemiptera are terrestrial and phytophagous; only the Heteroptera include groups which are carnivorous, many of which are also aquatic.

This is an old order, since, by the lower Permian, the Archescytinidae (Fig. 6.25D, E) were represented. Heteropteran Progonocimicidae (Fig. 6.25K) were well established in the late Permian. Extensive diversification occurred in the Mesozoic in association with the emergence of the flowering plants.

Excellent accounts of the Hemiptera have been given by Pesson (1951) and Poisson (1951).

Anatomy of Adult

Head (Fig. 30.1). Opisthognathous in Sternorrhyncha and Auchenorrhyncha, with mouth-parts emerging from near rear of head; prognathous in most Heteroptera due to development of a sclerotised gula ventrally between

insertion of the mouth-parts and base of head; some Heteroptera (e.g. Peloridiidae and Corixidae) have both gula and opisthognathous appearance. Antennae mostly 3–10-segmented. Compound eyes various, sometimes absent. Two ocelli present, or 3 in Psylloidea, Aphidoidea, Cicadoidea, a few Fulgoroidea, or absent, as in many Nepomorpha, Tingidae, Aradidae, most Miridae, Largidae, Pyrrhocoridae and some flightless species and morphs. Persistent nymphal eyes and accessory eyes present in some adult Sternorrhyncha.

Mouth-parts (Figs 30.2, 62) modified to form 2 pairs of sclerotised, flexible, often apically barbed stylets (mandibular and maxillary stylets), lying in an anterior groove in 1–5-segmented labium (*rostrum*). Mandibular stylets lateral to maxillary stylets. Longitudinal grooves on inner aspect of each maxillary stylet form a posterior salivary canal and an anterior food canal between apposed stylets. Stylets articulate inside head with internal surfaces of maxillary and mandibular plates (*lora*; paraclypei) by means of maxillary and mandibular levers. Lora continuous medially with hypopharynx, which forms the floor of the sucking pump (cibarium). Salivary syringe located in hypopharynx. Epipharynx forms roof of cibarium. Only the stylets penetrate the plant or host tissue; labium may shorten to allow stylet penetration; in Aphididae and adult Aleyrodidae, 2nd labial segment

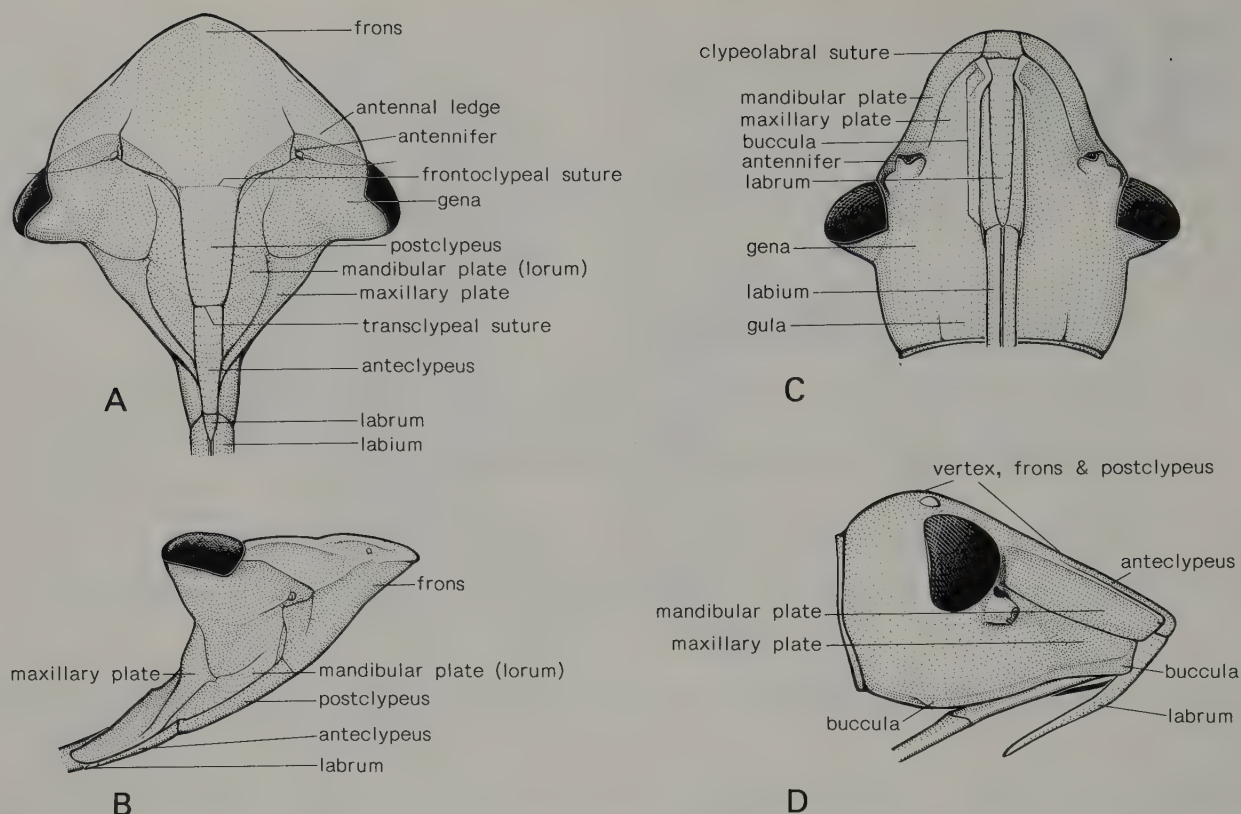


Fig. 30.1 Heads: A, *Stenocotis depressa*, Cicadellidae, frontal; B, same, lateral; C, *Nezara viridula*, Pentatomidae, ventral; D, same, lateral. [S. Monteith]

retractible into basal segment; in most Auchenorrhyncha and Heteroptera labium bends posteriad. When much longer than labium, stylets may be held coiled or looped inside body, within an invaginated integumental fold (*crumena*) or an external diverticulum, as in adult Psylloidea, Adelgidae, Enicocephalidae, Aradidae, Termitaphididae, Cydnidae, Plataspididae. Mouth-parts absent in all male and some female Coccoidea and sexuales of some Aphidoidea.

In most Heteroptera a pair of ventral, keel-shaped flanges (*bucculae*) present, one on each side of resting labium. Labrum usually small, triangular; covers stylets and labium basally; epipharynx may project from under and beyond labrum. Clypeus large, especially in Auchenorrhyncha, and frequently divided into anteclypeus and postclypeus by transclypeal suture. Postclypeus (considered by some authors to be the frons) accommodates dilator muscles of sucking-pump, and may be continuous with reduced frontal region or separated from it by frontoclypeal (epistomal) suture. Genae produced anteriorly in many Psylloidea to form prominent paired lobes. Tentorium complete in Sternorrhyncha, Cicadoidea, Cercopoidea, Peloridiidae; slender, unipartite, comprising a transverse body posteriorly, and posterior and anterior arms. Reduced in other Auchenorrhyncha and some Nepomorpha, absent in most other Heteroptera. [Matsuda 1965; Hamilton 1981]

Thorax (Fig. 30.3). Pronotum variously developed, commonly extended (e.g. Membracidae, Tingidae); lateral

paranotal extensions present, e.g. in Peloridiidae and Cicadellidae (Myerslopiini and Monteithiini). Mesonotum large and usually with all the primary subdivisions; tegulae present in most Sternorrhyncha and Fulgoroidea. Mesoscutellum (called scutellum) posteriorly produced and spiniform in some Machaerotidae; usually large and triangular in Heteroptera; in some Pentatomoidea extends to posterior end of abdomen, covering wings at rest.

Propleura evident in some Sternorrhyncha, most Auchenorrhyncha, Dipsocoroidea and Peloridiidae, and each usually divided into episternum and epimeron; in other Sternorrhyncha more or less fused with pronotum or prosternum, and in other Heteroptera largely effaced by the extension ventrally of pronotum. Mesopleura and metapleura usually defined in Cicadelloidea, metapleura obscured by enlarged hind coxae. In Heteroptera, mesepisterna and metepisterna more or less obscure corresponding epimera; in most adult Heteroptera internal scent efferent glands open in metasternal and metepisternal regions and often provided with 'evaporative' areas (p. 435). Metathoracic furcae well developed in some saltatorial groups e.g. Psylloidea. Sterna usually small. Thorax modified in flightless forms, very reduced in apterous Sternorrhyncha. Meso- and metathoracic spiracles present in all Hemiptera.

Legs. Legs of most Hemiptera cursorial and similar. Fore legs of some predacious Heteroptera raptorial, e.g. Enicocephalidae (Fig. 30.47), Nepomorpha (Figs 30.54, 55, 56B) and some Reduviidae. Adhesive pad (*fossula*

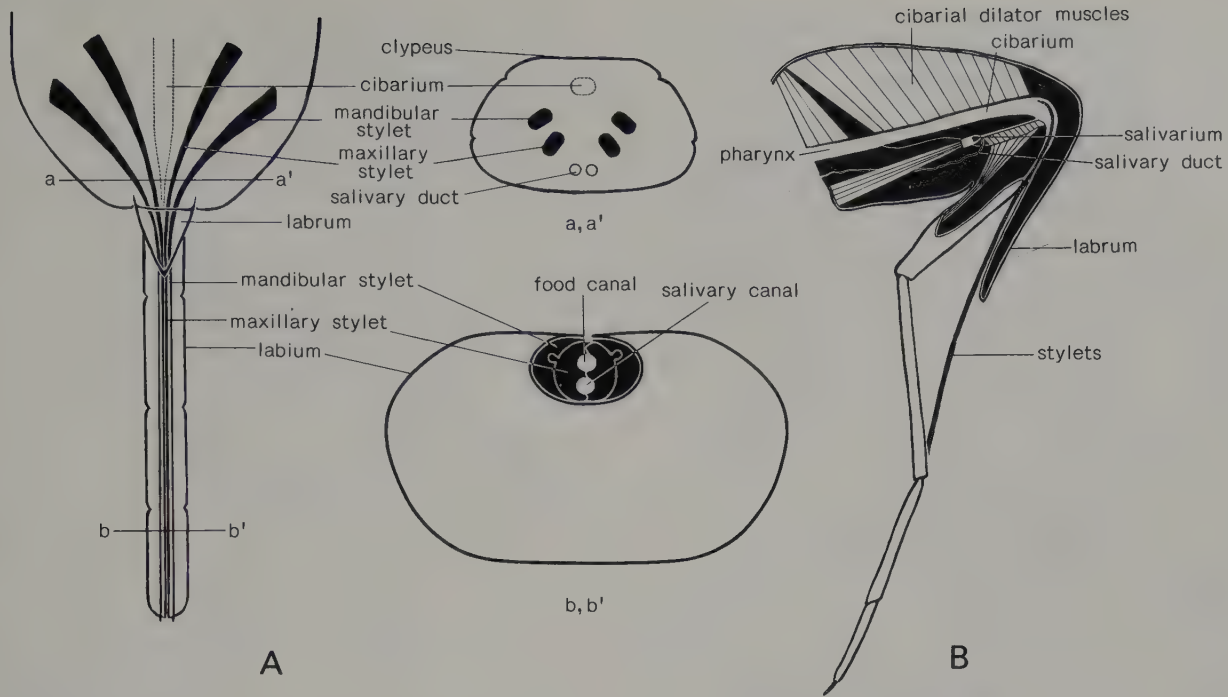


Fig. 30.2 Mouth-parts: A, diagram of principal parts and transverse sections through a-a' clypeal region, b-b' labial region; B, diagrammatic longitudinal section showing relationships of cibarium, pharynx, and salivarium. [S. Monteith]

spongiosa) subapically on fore and sometimes mid tibia of Nabidae, Anthoridae and some Reduviidae used for holding prey. Fore legs of Corixidae short, and tarsus modified as hair-fringed scoop (*pala*) (Fig. 30.57B). Many Gerromorpha have long, very slender legs for moving over water surfaces (Fig. 30.51), and many aquatic Heteroptera have at least the hind legs modified for swimming with the tibiae in particular often flattened and fringed with long hairs (Figs 3.7, 30.54D, 57A). Hind legs of Psylloidea, Aleyrodoidea, Auchenorrhyncha (except Cicadoidea) adapted for jumping; tibial and tarsal apices may be strongly spinulose (Fig. 30.37). Some Heteroptera (e.g. Schizopteridae, halticine Miridae) also jump, using hind legs; some Aphidoidea jump with fore legs. Legs of most Cydnidae, some Margarodidae fossorial. Legs of many female Coccoidea reduced or absent (Fig. 30.24).

Coxae either free or fixed; hind coxae of Cicadelloidea form immobile transverse plates covering most of ventral

metathorax (Fig. 30.31E). Pair of spiculate pads present medially on hind coxae of most Schizopteridae. Trochanters sometimes fused with femora e.g. Aphidoidea and many Aradidae. Sole bladder at apex of tibiae in some Aphidoidea. Tarsi maximally 3-segmented in Auchenorrhyncha and Heteroptera, maximally 2- in Sternorrhyncha. In *Diaprepocoris* (Corixidae) overlapping cuticular blades present in addition to swimming hairs on hind tarsi as a swimming aid. Pretarsal claws, usually 2; only 1 in Coccoidea, some Enicocephaloidea and Nepomorpha, absent from fore or hind legs or both of some Gerromorpha. Other pretarsal structures are diverse and often of uncertain homology: single empodium arising from unguitractor plate in Aleyrodidae and Tettigarctidae (but absent in Cicadidae), pair of setiform empodia (parempodia) in Aphidoidea and many Cimicomorpha; cushion-like, simple or bilobed arolium in many Psylloidea and saltatorial Auchenorrhyncha. In

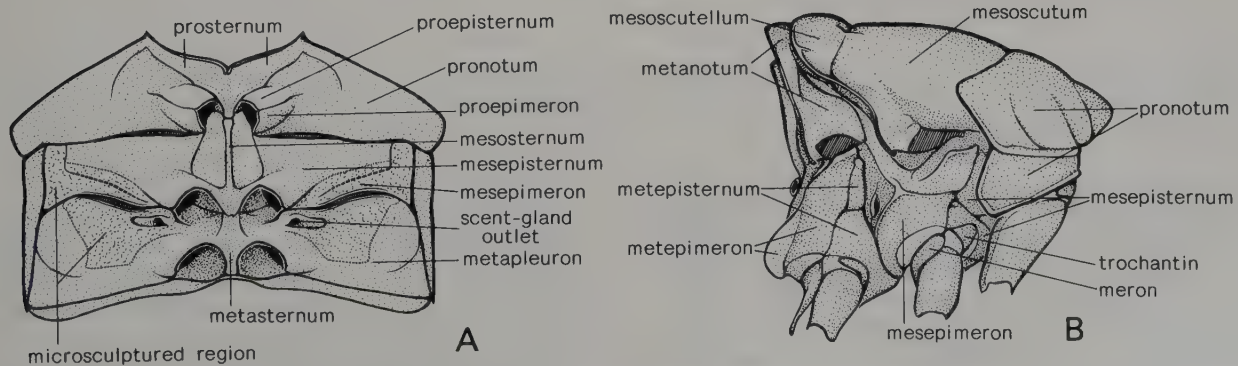


Fig. 30.3 Thorax: A, ventral aspect of *Nezara viridula*, Pentatomidae; B, lateral aspect of *Cystosoma saundersii*, Cicadidae. [S. Monteith]

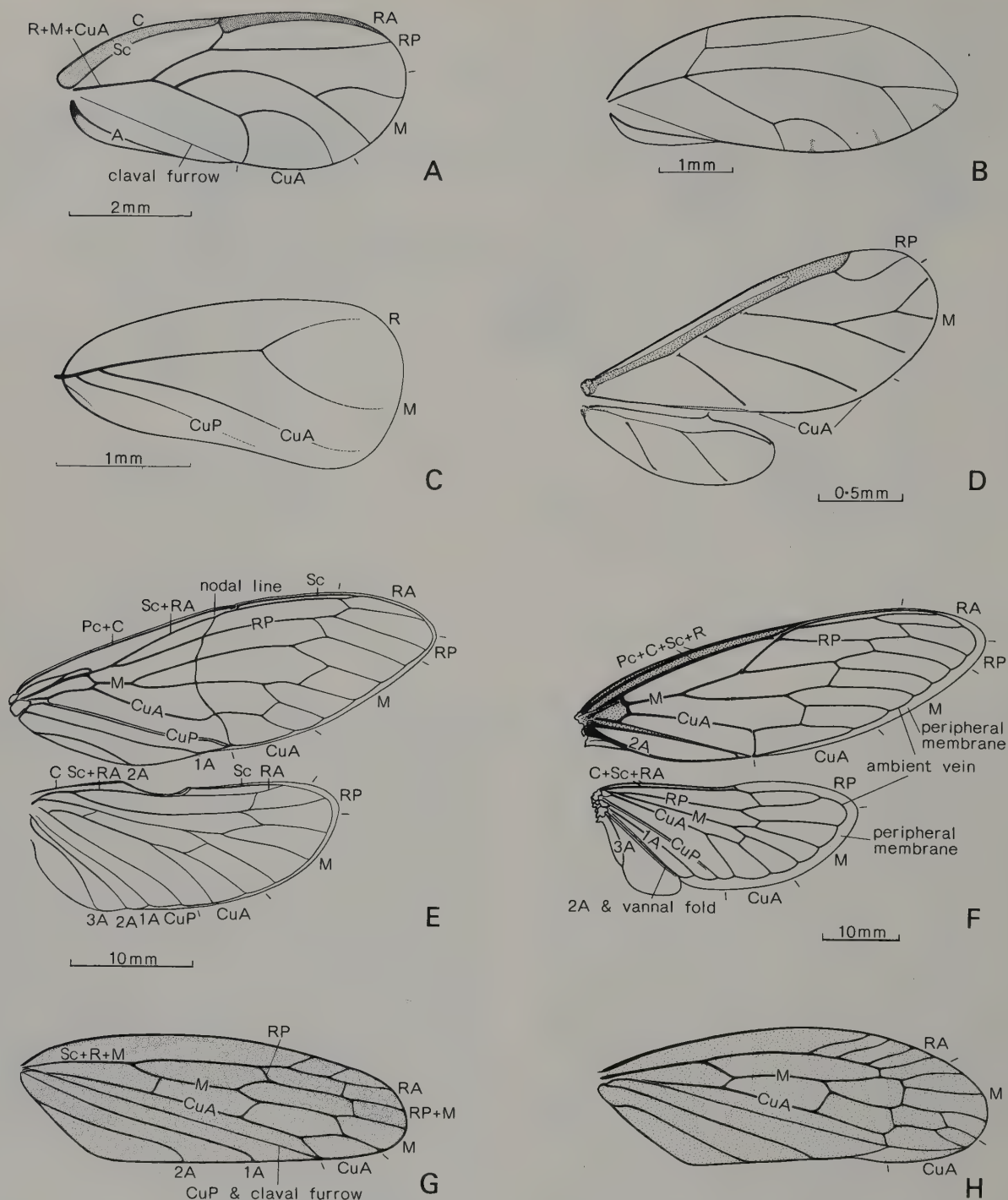


Fig. 30.4 A, fore wing of *Acizzia acaciaedecurrentis*, Psyllidae; B, same of *Trioza eugeniae*, Triozidae; C, same of *Synaleurodicus* sp., Aleyrodidae; D, fore and hind wings of *Aphis acaenoviniae*, Aphididae; E, same of *Tettigarcta tomentosa*, Tettigarctidae; F, same of *Cyclochila australasiae*, Cicadidae; G, fore wing of *Putoniessa nigra*, Cicadellidae; H, same of *Australoscopus* sp., Eurymelidae. [A–C by T. Nolan; D, E, G, H by S. Monteith; F by S. P. Kim]

addition to paired, usually setiform parempodia, Gerromorpha have a dorsal and a ventral, usually lamellate, arolium; these and the claws may be modified to form swimming blades or fans (Veliidae). Pentatomomorpha have 2 pulvilli (of ungual origin). Miridae have lamellate (Figs 30.60A, B) or setiform (Figs 30.60C–F) parempodia. They often have fleshy pulvilli,

which originate either on the ventral surface (Figs 30.60A, B, D) or inner surface of the claws, or pseudopulvilli, which arise distally on the unguitractor plate (Fig. 30.60C). [Fennah 1945; Goel and Schaefer 1970; Goel 1972; Schuh 1976; N. M. Andersen 1982]

Wings (Figs 6.25; 30.4, 5, 25A). Differ considerably within the order. In repose, held roofwise (tectiform) over

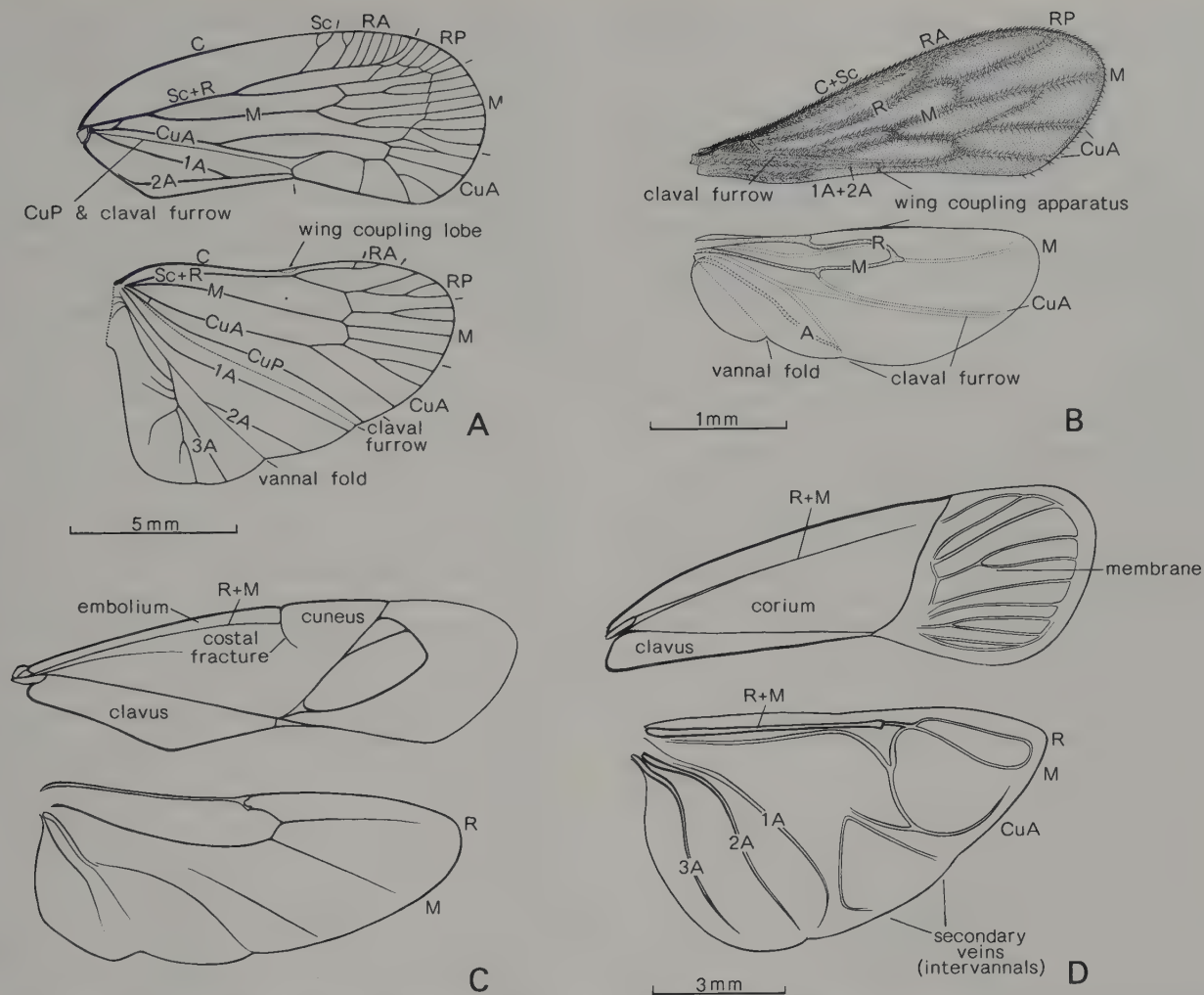


Fig. 30.5 A, fore and hind wings of *Achilus flammeus*, Achiilidae; B, same of *Oncycotitis* sp., Enicocephalidae; C, same of *Creontiades* sp., Miridae; D, same of *Nezara viridula*, Pentatomidae. [A, B by S. P. Kim; C, D by S. Monteith]

body in most Sternorrhyncha (Psylloidea, most Aphidoidea) and Auchenorrhyncha; lie flat over abdomen and overlap apically in most Heteroptera; coleopteroid in some (e.g. some Issidae, Schizopteridae and Lygaeidae). Fore wings of homogeneous, membranous to coriaceous texture in Sternorrhyncha, Auchenorrhyncha, Peloridiidae, Enicocephaloidea, Dipsocoroidea and most Gerromorpha, but in other Heteroptera, except where secondary reduction has occurred (e.g. Tingidae), apex distinctly more membranous than coriaceous base. Flexion line (*claval furrow*) delimits a *clavus* in anal area; *clavus* lies alongside scutellum when wing in repose; absent in Aphidoidea. In Auchenorrhyncha (Figs 30.4E–H, 5A) venation well developed; complete venation, including a conspicuous nodal line, observable in the primitive cicada *Tettigarcta* (Fig. 30.4E), ambient vein commonly present in Cicadomorpha; secondary vein proliferation common, especially in Fulgoroidea. Fore wings of Sternorrhyncha commonly membranous; venation simple in Psylloidea (Figs 30.4A, B), ambient peripheral vein present; venation very reduced in Aleyrodidae and Coccoidea (Fig. 30.4C). In Heteroptera, peripheral vein present in Peloridiidae,

Enicocephaloidea, Dipsocoroidea. The typical heteropterous fore wing (*hemelytron*) (Fig. 30.5D) structured for both protection and flight; has reduced venation, and 3 distinct regions: *corium*, *clavus* and membranous portion (*membrane*). In some Cimicomorpha (Fig. 30.5C), *corium* further divided into *embolium*, anterior to R+M, and *cuneus*, defined by *costal fracture*. Hind wings membranous, reduced in Sternorrhyncha; absent in Coccoidea and some flightless species. Vannus present in Auchenorrhyncha and Heteroptera, folded under rest of wing in repose by means of vernal fold. Venation well developed in Auchenorrhyncha; ambient vein present in Cicadomorpha; venation reduced in Heteroptera. Both fore and hind wings used in flight. Wing coupling mechanism absent in Aleyrodidae; hind wings operating independently of fore wings. Coupling by means of interlocking areas on posterior and anterior margins of fore and hind wings, respectively, in other Sternorrhyncha and in Auchenorrhyncha (Ossiannilsson 1950), and by a gripping device under fore wing *clavus* in Heteroptera. Aptery and brachyptery widespread; not known in Psylloidea and Aleyrodidae. Wing autotomy (self de-

alation) common in Gerromorpha (N. M. Andersen 1982). [Shcherbakov 1981, 1982; Wootton and Betts 1986; Dworakowska 1988]

Abdomen. Basal segment petiolar in Aleyrodidae; otherwise broadly and closely associated with metathorax. Heteroptera usually with *connexivum* on each side of abdomen, each tergite being divided laterally and longitudinally into 1, sometimes 2, pairs of laterotergites or paratergites attached by membrane to main tergite. Connexivum allows increased distension of abdomen. Segment 10 in both sexes usually modified as anal tube (*proctiger*), well developed in many Psylloidea and Auchenorrhyncha. Abdomen in many Sternorrhyncha soft bodied and with ill-defined segmentation; perianal structures (circumanal wax glands, vasiform orifice, cauda, anal tube) often developed for removal of excreta.

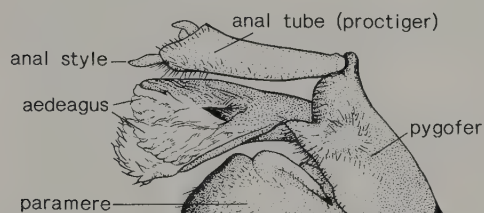
Eight pairs of abdominal spiracles usually present; 7 pairs usual in Aphidoidea, and in some Dipsocoromorpha, Gerromorpha and Cimicomorpha, and in the primitive coccoid families Margarodidae and Ortheziidae; absent in all other Coccoidea; 3 pairs in many Schizopteridae; 2 pairs in Aleyrodidae and these do not connect transversely or with thoracic tracheae. Spiracles ventrally placed but some located dorsally on connexivum in some Lygaeidae and Leptopodoidea.

Aquatic bugs (Nepomorpha) have developed various

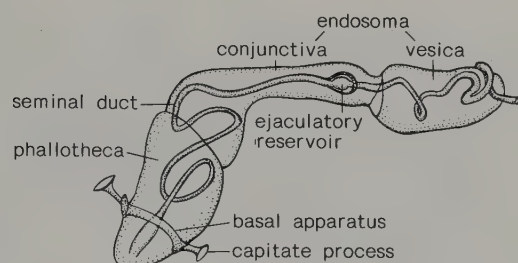
modifications for aerobic respiration under water. Corixidae take air into space between head and pronotum. In Naucoridae, an air bubble is carried by a hairy plastron concentrated on venter. In Notonectidae, the spiracles lie in hair-lined, ventrolateral respiratory channels. In Belostomatidae, spiracles of T8 lie at base of 2 dorsoventrally flattened, strap-like appendages forming a short, retractile siphon. In Nepidae, the single large spiracle of T8 lies at base of an apical cylindrical siphon formed of two closely apposed appendages. [Thorpe 1950]

GENITALIA (Fig. 30.6). Except in Sternorrhyncha and some Aenictopecheidae, which have an external aedeagus (penis), segment 9 of male usually modified into a capsule-like *pygofer* (pygophore) accommodating an aedeagus of varied and often complex structure, and a pair of *parameres* (claspers, harpagones, gonostyli). Parameres asymmetrical in some Cimicomorpha and Nepomorpha, sometimes single; reduced in many Enicocephalidae; absent in Coccoidea, some Enicocephalidae and Thaumastocoridae. Additional parameres, often asymmetrical, occur, e.g. in many Dipsocoroidea. [Cobben 1968, 1978]

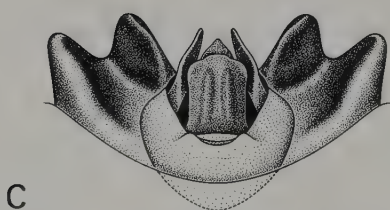
Three pairs of *valvulae* (gonapophyses, gonostyli) arising from *valvifers* (gonocoxae) present in Psylloidea, Aleyrodidae, Auchenorrhyncha and *Diaprepocoris* (Corixidae), 2 in most other Heteroptera. Structure of *ovipositor* usually related to mode of oviposition. Well-



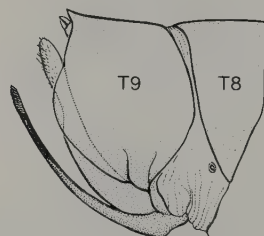
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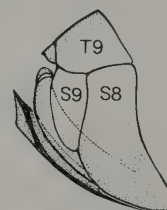
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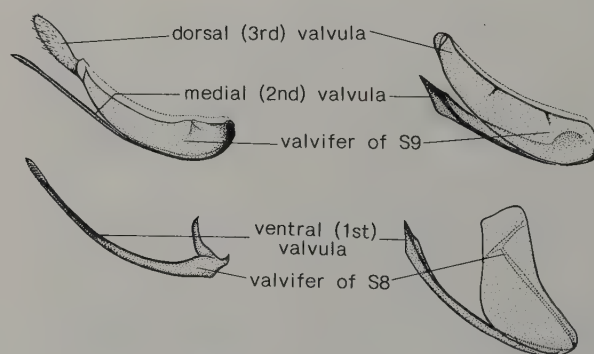
C



D



E



F

Fig. 30.6 A, ♂ terminalia of *Desudaba psittacus*, Fulgoridae; B, aedeagus of *Nysius cleavelandensis*, Lygaeidae; C, pygofer of *Poecilometis patruellis yni-grum*, Pentatomidae, dorsal aspect; D, ovipositor, and parts separated, of *Cystosoma saundersii*, Cicadidae; E, same of *Creontiades* sp., Miridae; F, ovipositor of *Nezara viridula*, Pentatomidae, ventral aspect.

[A, B, D–F by S. Monteith; C by S. P. Kim]

developed, often laciniate ovipositor present (some Psylloidea, most Auchenorrhyncha, Notonectidae, Cimicoidea, Pentatomomorpha) where oviposition is penetrative e.g. into plant tissues. When eggs laid superficially, ovipositor usually short (many Heteroptera) or absent (Coccoidea, most Aphidoidea). [Scudder 1959]

Trichobothria (Figs 30.70B, 74, 76B, 77B). Specialised sensory hairs occur in many Heteroptera; the number, type and distribution of these hairs are of considerable phylogenetic and taxonomic importance. May arise from pit in, or domed area on, integument; surrounding integument may be ornamented or otherwise differentiated. [Schuh 1975]

Glands and Associated Structures. Complex wax-producing glands present in many Sternorrhyncha and some Fulgoroidea.

Scent gland system (Figs 2.40; 30.3, 7, 76B, c). A fundamental feature of Heteroptera. In nymphs, 0–4 primitively intersegmental glands, or secondarily paired glands, located dorso-abdominally, opening medially on or between T3–T7, often reduced in number and size or absent, especially in aquatic forms. Nymphal glands may remain functional in adult e.g. in some Enicocephalidae, Dipsocoroidea and Gerromorpha; in other adults their position in previous instars often marked by prominent plaques. In adult Heteroptera the system is located ventrally, usually in metathorax; primitively consists, as in Enicocephalidae, Dipsocoroidea, of unpaired, median, integumentary invagination at junction of metasternum and abdomen forming internal sac of secretory cells surrounding a lumen (reservoir). The most advanced system occurs in terrestrial bugs (Cimicomorpha, Pentatomomorpha) where a pair of glands and separate, single or paired reservoirs open laterally by a pair of valved orifices into peritremes surrounded by elaborately microsculptured areas in metepisternal region. The glands function principally as organs of chemical defence against predation but may also produce pheromones involved in aggregative, warning and/or precopulatory behaviour. Other types of scent glands (Brindley's glands, Carayon's glands) present in some Reduviidae, Pachynomidae, Tingidae and Thaumastellidae. [Carayon 1971; Cobben 1968, 1978; Staddon 1979, 1986; Aldrich 1988; Carver 1990]

Protrusible pregenital glands present in some Saldidae.

Acoustic and vibrational systems. Auchenorrhyncha have complex sound-producing and sound-receiving mechanisms, the principal components of which are the tymbals and tympana, respectively, located dorso- and ventro-laterally in abdomen. Tymbals are possessed by both sexes though usually better developed in males, and absent in female Cicadidae. Distinctive tympana known only in male and female Cicadidae. The system is best developed in male Cicadidae (p. 465; Figs 2.30; 30.28). The loud songs of the large cicadas are well known, but smaller cicadas and other Auchenorrhyncha probably produce non-audible, acoustic signals transmissible via the plant substrate rather than through the air (Claridge 1985).

Diverse stridulatory mechanisms are known (Figs 2.29; 30.8), producing signals transmissible through air, plant

substrate and water. In many Reduviidae, the apex of the labium (plectrum) rubs against the transversely striated and grooved prosternum (stridulitrum); in male Corixidae, plectral spines on fore femora rub against the clypeal margin; in some Colobathristidae, against side of head. Alary (plectral)-thoracic (stridulitral) systems are known in Psylloidea and Cicadoidea; alary-alary in Cicadoidea; crural (leg)-thoracic in Aradidae, Lygaeidae; crural-abdominal in Pentatomorpha, Veliidae, Aradidae, Corixidae, Miridae and *Toxoptera* (Aphididae); abdominal-thoracic and abdominal-alary in Pentatomorpha; abdominal in Corixidae, Pentatomidae, Lygaeidae, Coreidae and Reduviidae; and aedeagal-pygophoral in Scutelleridae. Rocking, knocking and oscillating movements are probable examples of vibrational signalling. Some Gerridae communicate by generating surface ripples in the water (Wilcox 1972). [Ashlock and Lattin 1963; Boulard 1976; Schuh 1974, 1984; Gogala 1988; K. L. Taylor 1985; Aiken 1985]

Internal Anatomy. The sucking pump is the cibarium (Fig. 30.2B); pharynx small; true crop absent. Salivarium specialised as salivary pump; anterior end of its outlet duct projects into base of lumen of maxillary salivary canal. Paired salivary (labial) glands (Figs 30.9A–C) in thorax typically comprise, on each side, a principal and an accessory gland, the ducts of which unite to open as a common duct into salivary pump. Principal gland simple, bipartite or bilobed, or (in most Auchenorrhyncha) multilobed; histologically diverse. Accessory gland vesicular or tubular. Two pairs of glands in Schizopteridae. [Miles 1972; Cobben 1978]

Mid gut (Figs 30.9D–E) frequently differentiated into at least an anterior crop-like dilation and posterior tubular region. Long, anteriorly produced diverticulum of unknown function present in Fulgoroidea. Filter system present to varying degrees in many Sternorrhyncha and Auchenorrhyncha (p. 439). Peritrophic membrane absent. Four Malpighian tubules usually present in Auchenorrhyncha and Heteroptera, sometimes united basally in pairs; fewer in Sternorrhyncha, absent in Aphidoidea. In Diaspididae (Coccoidea) mid gut not connected with hind gut (or Malpighian tubules). Anus absent in Phylloxeridae (Aphidoidea).

Ventral ganglia concentrated; number of centres range from one, as in most Hemiptera, to 4 (suboesophageal, prothoracic, mesothoracic and metathoracic-abdominal) as in Tettigarctidae, Cercopidae, Peloridiidae, Schizopteridae.

REPRODUCTIVE SYSTEM. (Fig. 30.10). Number of ovarioles ranges from 1 to more than 100 per ovary in Auchenorrhyncha and Sternorrhyncha, with intraspecific variation common in Aphidoidea; 2–8, usually 7, per ovary present in Heteroptera with the number constant for a species (Pendergrast 1957). Ovarioles acrotrophic. Spermathecae 0–3, usually 1; simple or complex, absent in Cimicomorpha, but replaced in some Cimicoidea by analogous structures (seminal conceptacles, pseudospermathecae) (Carayon 1954). *Spermalège* (Fig. 30.13) present in many Cimicoidea (p. 440). Testes each have 1–8 follicles. Accessory glands present in both sexes.

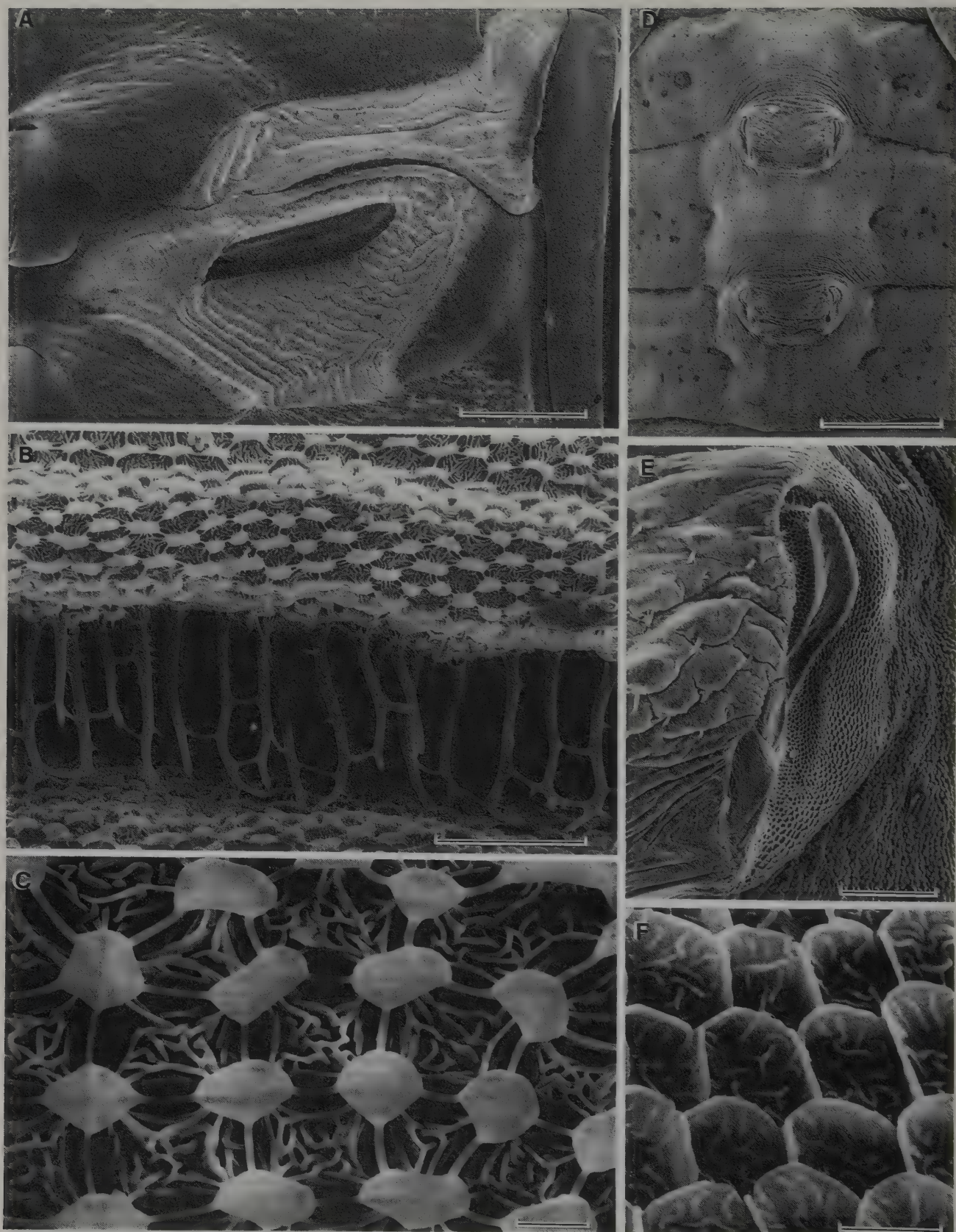


Fig. 30.7 External apparatus of scent gland system of Heteroptera. A–C, *Poecilometis longicornis* (Pentatomidae), adult. A, left side of mesepisternum and metepisternum showing ostiole, dispersal channel, intersegmental opening to spiracle II, surrounding microsculpture (lighter coloured area) (scale = 1 mm); B, detail of spiracular opening and surrounding microsculpture (scale = 50 μ m); C, detail of mycoid microsculpture (scale = 5 μ m). D–F, *Amorbus* sp. (Coreidae), final instar nymph. D, dorsal view of abdomen, showing glands T4–5 and T5–6 (scale = 1 mm); E, detail of gland T4–5 showing dispersal channels and microsculpture of right-hand outlet (scale = 100 μ m); F, detail of microsculpture (scale = 5 μ m). [H. Geier]

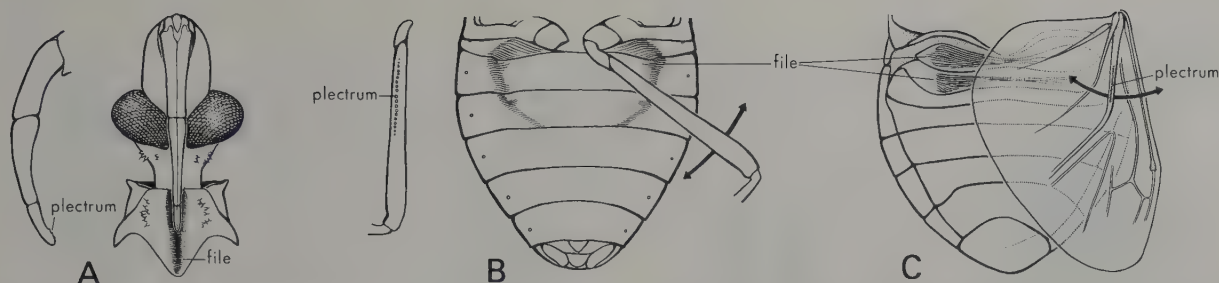


Fig. 30.8 Stridulatory mechanisms of Heteroptera: A, *Oncocephalus confusus*, Reduviidae; B, *Oncocoris punctatus*, Pentatomidae; C, *Aethus indicus*, Cydnidae. [S. Monteith]

Karyotype. Chromosomes holocentric. Usually 5–16 haploid autosomes, but the number may vary from 2 (some Aphidoidea and Coccoidea) to 26 (some Heteroptera). The usual sex-chromosome system is XO in Sternorrhyncha and Auchenorrhyncha and XY in Heteroptera; X may be multiple (Ueshima 1979). Coccoidea have some unusual sex-determining mechanisms (Nur 1980).

Immature Stages

Egg (Fig. 30.11). Ovoid with simple chorion in most Sternorrhyncha and Auchenorrhyncha; those of Aleyrodidae and Psylloidea pedunculate, the peduncle being inserted into host plant, from which water is absorbed.

Eggs of many Heteroptera have an operculum (especially well developed in Cimicomorpha) and hollow chorionic processes (aeropyles) of varying shape and length; those of Nepidae have apically plastronic horns at anterior pole. [Southwood 1956; Cobben 1968]

Nymph (Fig. 30.12). Most Hemiptera typically hemimetabolous. Number of nymphal instars, 2–7, usually 5. Nymphs usually lack ocelli, and may have fewer tarsal and antennal segments than adults. Wax production common in Sternorrhyncha and Fulgoroidea, often in form of long filaments. Heteropteran nymphs possess dorsal abdominal scent glands; lack ventral thoracic glands characteristic of adult. Except in Sternorrhyncha, nymphs generally resemble adults in structure and habit.

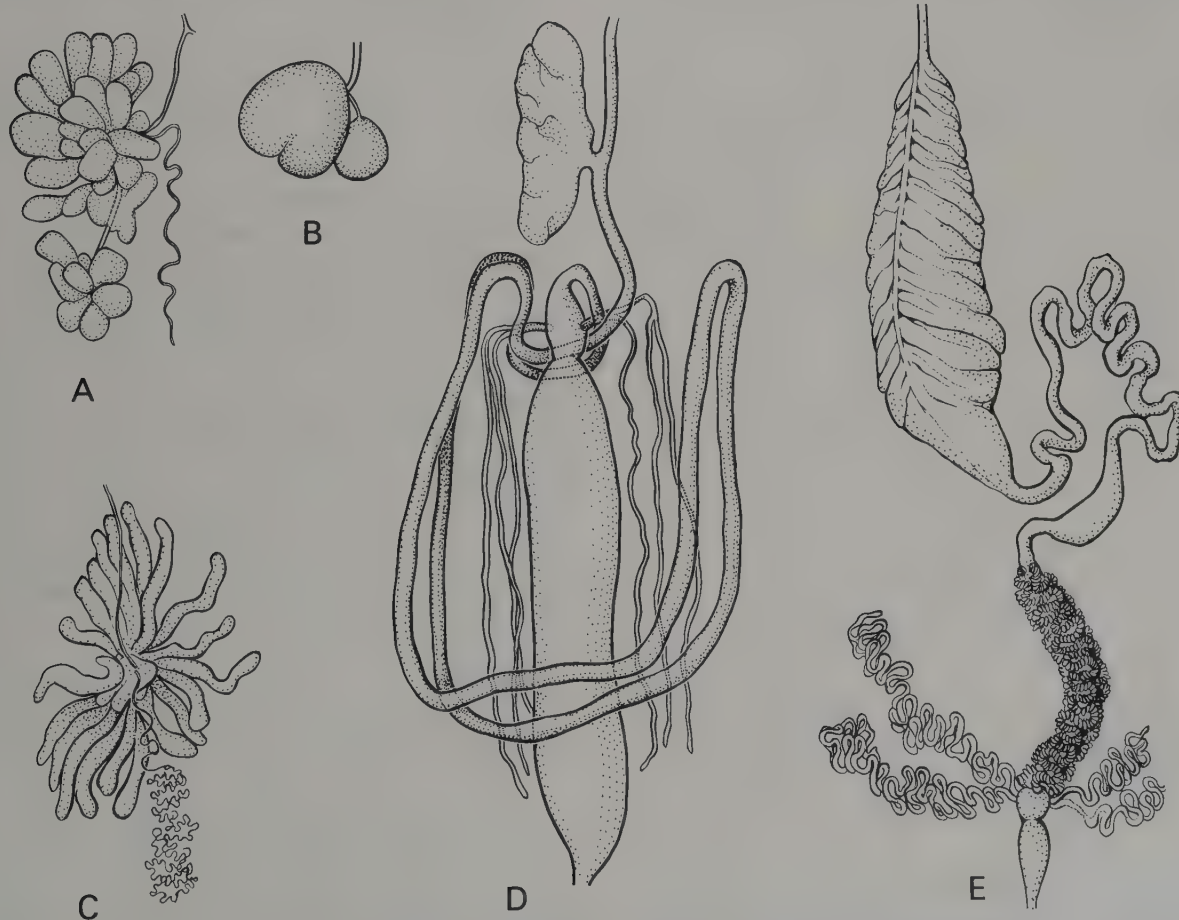


Fig. 30.9 Digestive system: A, salivary glands of *Cystosoma saundersii*, Cicadidae; B, same of *Macrosiphum rosae*, Aphididae; C, same of *Tectocoris diophthalmus*, Scutelleridae; D, alimentary canal of *Dardus* sp., Eurybrachyidae; E, same of *Tectocoris diophthalmus*, Scutelleridae. [S. Monteith]



Fig. 30.10 Reproductive system of: A, ♂, B, ♀, *Tectocoris diophthalmus*, Scutelleridae; C, ♂, D, ♀, *Cicadetta* sp., Cicadidae. Spermathecae: E, *Nezara viridula*, Pentatomidae; F, *Mictis profana*, Coreidae; G, *Metacanthus pluto*, Berytidae. [S. Monteith]

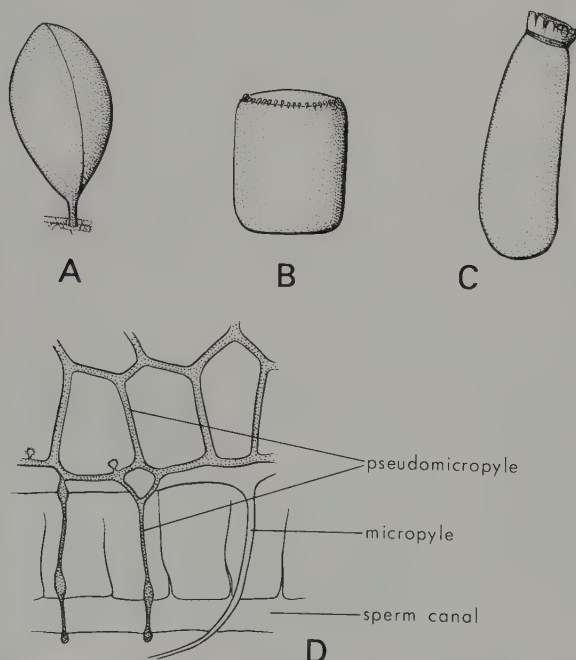


Fig. 30.11 Eggs of: A, *Cardiaspina albicollaris*, Psyllidae, height 0.35 mm; B, *Nezara viridula*, Pentatomidae, height 1 mm; C, *Pristhesancus plagipennis*, Reduviidae, height 2 mm; D, surface view of base of micropylar region of *Rhinocoris* sp., Reduviidae (after Southwood 1956). [S. Monteith]

Any major differences, or differences between the nymphal instars themselves, reflect different habits. First instars of Coccoidea and Aleyrodidae highly mobile, with well-developed appendages; subsequent instars usually sedentary, with reduced or atrophied appendages (Figs 30.16, 17, 21, 22). Nymphs of Psylloidea may differ markedly from their adults (p. 448); those of many Spondyliaspidae live under tests (lerps) produced from anal excretion (Figs 30.15F–H, 16A–D). The subterranean cicada nymph differs from the terrestrial adult in having large, fossorial fore legs (Fig. 30.27C). Nymphs of Cercopoidea are relatively soft bodied and live in 'spittle' or in calcareous tubes (Fig. 30.29). Apical abdominal segment(s) of nymphs of Membracidae telescoped within preceding segment at rest; eversible to form an 'anal whip' (Fig. 30.35).

DeCoursey (1971) and Herring and Ashlock (1971) provided keys to families and subfamilies of nymphs of North American Heteroptera.

Biology

Feeding. Sternorrhyncha and Fulgoroidea feed predominantly in phloem, and Cicadoidea and Cercopoidea in xylem. Cicadelloidea feed in phloem (e.g. Membracidae, deltocephaline Cicadellidae), in xylem (Cicadellinae) or in parenchyma (typhlocybine Cicadellidae).

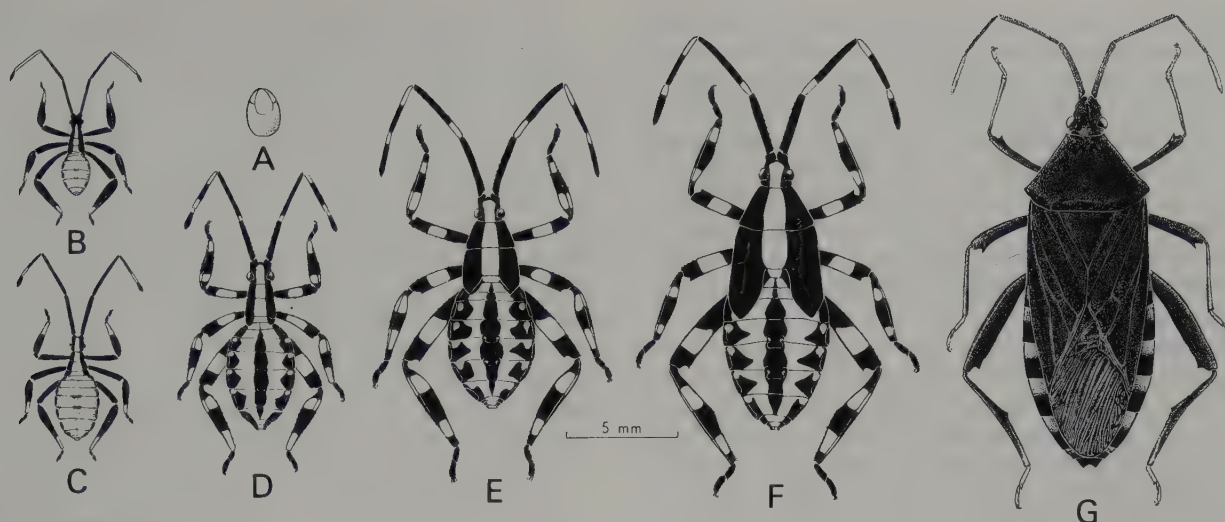


Fig. 30.12 A–G, egg and instars of *Amorbus alternatus*, Coreidae.

[S. Monteith]

Phytophagous Hemiptera feed in parenchyma, plant seeds or pollen; and predacious or parasitic Hemiptera in invertebrate and vertebrate tissue and blood.

Associated with the sucking habit and liquid diet of Hemiptera are specialised features, notably the piercing-sucking mouth-parts, sucking pump, complex salivary glands, stylet sheath and alimentary filter system (Fig. 2.43). To feed, the stylets may probe within the host in search of a specific feeding site, but the means of motivation and site location are not clearly understood. Saliva is pumped down the posterior channel of the maxillary stylets and the liquid or particulate food is sucked up the anterior one. During penetration of the stylets into a host plant, one of the salivary secretions may gel upon extrusion, thus forming a flange to the puncture hole and a firm lining (*stylet sheath*) to the path of the stylets through the plant tissue to the feeding site. The sheath is eventually left behind in the plant upon withdrawal of the stylets, as a permanent stylet track. The stylet sheath is characteristic of the phloem- and xylem-feeding Sternorrhyncha and Auchenorrhyncha, and may also be produced by some Pentatomomorpha when probing some distance into the plant. Most Hemiptera employ instead a 'lacerate-and-flush' method of feeding, whereby the stylets are used to lacerate and the saliva to macerate and dilute the tissue to a suckable brew.

The lipoproteinaceous stylet sheath material is secreted by the anterior lobe of the principal salivary gland; digestive enzymes and the anticoagulants of haematophages, by the posterior lobe. The watery saliva of the accessory gland is the flushing agent, and is also gustatory and sometimes excretory in function (Miles 1972).

Many Sternorrhyncha and Auchenorrhyncha have developed in diverse ways an *alimentary filter system* (Fig. 2.43) in which an anterior part of the gut is permanently encapsulated by, or is in close apposition to, a posterior part (many Sternorrhyncha) or vice versa (many Auchenorrhyncha). Plant sap has a high water and carbohydrate : nitrogen ratio and the filter system allows sur-

plus water and sugars to be absorbed and passed speedily to the hind gut, leaving more useful components such as amino acids to pass into the main digestive region.

Endosymbiosis. Most Hemiptera have an obligatory, symbiotic relationship with host-specific, transovarially transmitted yeasts and bacteria. In Sternorrhyncha, Auchenorrhyncha, Peloridiidae and Cimicidae, the symbionts are for the most part contained within specialised cells or mycetocytes aggregated to form mycetome organs in the haemocoel. In other Hemiptera the symbionts are usually found free in the gut or in specialised gut diverticula. They are believed to provide nutritional requirements not obtainable by the host from food or by synthesis.

Hosts. Among phytophagous Hemiptera, host relations range from high specificity, as in Psylloidea and Aphidoidea, to wide polyphagy. Hosts are principally flowering plants, especially dicotyledons. Some Aphididae, Coccoidea, Miridae and Alydidae (*Leptocoris* in Vanuatu) feed on ferns, Peloridiidae on mosses; Aradoidea and some Fulgoroidea (Derbidae, Achilidae) are mycetophagous; the cryptogamic hosts have presumably been acquired secondarily. Of the Hemiptera, the more primitive groups (Enicocephalidae, Dipsocoroidea, Gerromorpha and Nepomorpha) are predacious, as are all Reduviidae, many Cimicoidea, some Miridae, some geocorine Lygaeidae and the *Asopus* group of Pentatomidae. Polyteneidae are ectoparasitic on bats and Cimicidae, triatomine Reduviidae and Cleradini (Lygaeidae) are blood-suckers of birds or mammals.

Habitat. Some Sternorrhyncha (not Aleyrodidae), a few Auchenorrhyncha and Tingidae induce gall formation in their hosts, ranging from leaf distortion and stem and root nodosities of some Aphidoidea to the complex, woody, sexually dimorphic galls of *Apiomorpha* (Coccoidea) (Figs 3.14; 30.25C, D). Subterranean living is common among Sternorrhyncha and nymphal Auchenorrhyncha (e.g. Margarodidae, Cixiidae, Cicadoidea) but not so common in Hemiptera (e.g. Cydnidae and the

extralimital Thyreocoridae). Among the Heteroptera are various degrees of adaptation to the aquatic environment. Most Saldoidea and Ochteroidea are littoral or intertidal. Most Gerromorpha are adapted for walking or skating over the surface of (usually fresh) water, but Haloveliinae (Veliidae), Hermatobatidae and Halobatinae (Gerridae) are marine, and some species of *Halobates* truly oceanic. A few wingless Mesoveliidae inhabit wet leaf litter or moss at high altitudes. The Nepomorpha (except Ochteroidea) are almost completely aquatic, the adults surfacing for air or dispersal flights.

Polymorphism (Figs 30.20, 21, 25, 50, 51). Polymorphism is widespread throughout the order. Sexual and alary polymorphism are often associated, e.g. in Coccoidea, where the female is apterous and larviform, and the male alate or alatiform. In Aphidoidea, polymorphism can also be, in various combinations, physiological, climatic, altruistic or nymphal (p. 454). Alary polymorphism may be associated with function, the apterous morph, for example, being specialised for reproduction (Coccoidea, Aphidoidea) and the alate for dispersal (Aphidoidea). The degree may be determined by environmental factors, as in Aphidoidea, Delphacidae and Cicadellidae. In Heteroptera it is more associated with habitat; brachyptery and aptery are common among ground- and litter-dwellers (Enicocephalidae, Anthocoridae, Aradidae, Lygaeidae); among the semiaquatic and aquatic Gerromorpha and Nepomorpha; and among ant mimics (Miridae). The termitophilous Termitaphididae and the ectoparasitic Cimicidae and Polyctenidae are apterous or micropterous.

Mimicry. Many of the large, stink-producing Heteroptera, especially among the Lygaeoidea and Pentatomoidea, and (predatory) Reduviidae are aposematically coloured, most commonly in red and black (Plate 3). Groups of these species, often in different families, share similar, apparently synaposematic, colour patterns. Many lygaeids, alydids and mirids are ant mimics; the smaller mirids are particularly difficult to distinguish from ants in the field. Other mirids are coleopteroid, or staphylinoid, or resemble Braconidae (Hymenoptera). Procrispis abounds. Many Cicadellidae, e.g. Cephalini, look like plant seeds, Membracidae mimic thorns and other plant parts, and Aradidae (bark bugs) resemble bark.

Reproduction. Most Hemiptera are oviparous, but most or all generations of Aphididae are viviparous, and Coccoidea may be oviparous, ovoviviparous or viviparous. All Polyctenidae are viviparous. Fertilisation in vitellarium and pre-ovipositional embryogenesis usual in Cimicoidea except Nabidae where fertilisation occurs near base of ovarioles. Some *Icerya* spp. (Coccoidea) are hermaphroditic. Arrhenotoky and thelytoky occur in some Aleyrodidae and Coccoidea, and either cyclical parthenogenesis or thelytoky, in Aphidoidea.

Copulation is effected in diverse ways; side by side as in many Cicadelloidea or end to end with one sex, usually the male, upside down as in some Fulgoroidea. In most aquatic Heteroptera the male mounts and remains on the female throughout coitus. In some terrestrial Heteroptera, however, the male dismounts after intromission and the

pair assume an end-to-end position facing in opposite directions; others (some Nabidae, Aradidae) copulate with their ventral surfaces apposed.

Anomalous and complex methods of insemination are usual in Cimicoidea; these methods are diverse but in none does the sperm enter the lumen of the mid section of the female genital tract. A spined aedeagus or modified paramere punctures the vaginal wall (prostemmatine Nabidae) or the external body integument (Anthocoridae, Plokiophilidae, Cimicidae, Polyctenidae), and sperm are deposited directly into the haemocoel, or indirectly via a specialised vaginal or integumental pouch (spermalège). At the time of oviposition, the sperm orientate towards and penetrate the wall of the genital tract. They proceed via blood-filled lacunae to the upper reaches of the genital tract, where they penetrate the lumen, thus effecting fertilisation. In some cases where the spermalège connects with the genital tract (Fig. 30.13) the sperm do not enter the haemocoel. Sperm may remain for long periods within the female awaiting egg maturation, either in the haemocoel, or within the wall of the genital tract or within the genital tract near the base of the ovarioles (Carayon 1964, 1966, 1977).

Life History. The eggs of many Coccoidea are protected under the body of the female, or in specially produced ovisacs; those of other Sternorrhyncha, and Fulgoroidea may be covered with wax. Those of many other Sternorrhyncha and Auchenorrhyncha, most Notonectoidea, Saldoidea and Cimicomorpha and some Lygaeidae are laid embedded in plant tissues or between plant parts. Most Coreoidea and Pentatomoidea glue their eggs, usually in groups, on leaves. Other Lygaeidae lay their eggs in the soil or surface litter, some Achilidae may drop them there, and many Cimicidae lay their eggs in crevices or on objects close to their host. The scutellerid *Tectocoris diophthalmus* and the tessaratomid *Erga longi-*

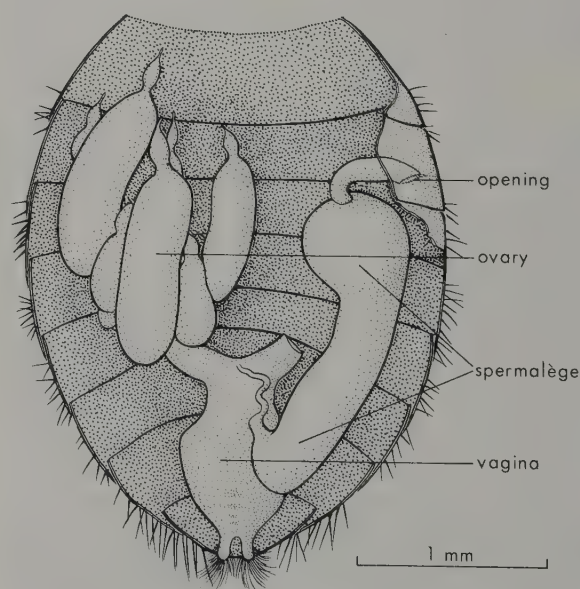


Fig. 30.13 Reproductive system of *Stricticimex brevispinosus*, Cimicidae, with right ovary removed.
[After Carayon 1964]

tudinalis and other Pentatomoidea exhibit maternal care by standing guard over their egg batches. Female *Diplonychus* and other Belostomatidae glue the eggs to the dorsum of the male parent, which assists in incubation (Fig. 30.55B).

The 1st instar of some Aphidoidea is specialised for dormancy; others are 'soldiers' (p. 454). Some margarodid Coccoidea undergo diapause underground as encysted nymphs, called 'ground pearls' (Fig. 30.22B). The major means of dispersal of Coccoidea and some pemphigine Aphidoidea is probably by the small, lightweight 1st instar, which is picked up and carried by air-currents.

A relatively prolonged, stationary instar, called a pupa, precedes the adult stage of Aleyrodidae and male Coccoidea, during which stage considerable metamorphosis takes place from the reduced, sedentary state to that of winged adult. Most presumptive male Coccoidea also have a prepupal stage.

Nymphs of many Hemiptera are gregarious, especially in the 1st instar. Those remaining gregarious to adulthood include *Oxycarenus* (Lygaeidae), ant-attended Eurymelidae and Membracidae, and soil-surface foragers such as *Nysius* (Lygaeidae) and *Leptocoris mitellatus* (Rhopalidae). Some Pentatomomorpha aggregate as adults. The largely sedentary and aggregative Aphidoidea and Coccoidea may build up large and dense local populations.

Honeydew. The sugar-rich excreta of many phloem-feeding Sternorrhyncha and Auchenorrhyncha are a valuable source of nutrition for other insects such as ants, honey bees and adults of some species predatory or parasitic as larvae (e.g. Neuroptera, Coccinellidae, Syrphidae, other aculeate Hymenoptera, Tachinidae). Honeydew is also consumed by some vertebrates, especially birds, and even humans. The manna of the Israelites was largely the honeydew of the pseudococcid *Trabutina mannipara* and, in Australia, lerps of spondylaspidine psyllids, which are derived largely from honeydew, were collected by Aborigines for food. [Bodenheimer 1951; Zoebelein 1956]

Mutualism. Ants are particularly attracted to sugars, obtained largely from honeydew and extrafloral nectaries. Fallen honeydew may be scavenged casually, but many ants, especially Myrmicinae, Dolichoderinae and Formicinae, have developed a mutualistic association (trophobiosis) with certain phloem-feeding Hemiptera, and solicit honeydew directly from the producer by means of antennal palpation. In certain associations the ants protect and promote those they solicit by moving them when warranted to more suitable feeding or sheltered sites on the plant or to and from the ant nest, or tend them permanently within the nest. Some ant queens (e.g. of *Acropyga* spp.) carry pseudococcids between their mandibles on nuptial flights.

In most associations, the ants, as natural aggressors and perhaps incidentally, provide significant protection to the honeydew producers they tend by killing or warding off parasites and predators. On occasion they also prey on the tended population, for instance, when it becomes uncontrollably large, or when individual hosts are uncharacteristically active or become isolated.

Many Aphididae, Coccoidea, cicadellid Xestocephala-

linae, Eurymelidae and Membracidae, and some Psylloidea and Aleyrodidae are solicited by ants. Whereas tended Hemiptera are consistent in their attractiveness, ants usually solicit a variety of species, albeit preferentially. The mutualism is commonly not obligatory, the degree of association varying according to sympatry, climate, availability of other food, nutritional requirements of the ant colony, and other factors.

Both ants and solicited species may exhibit behavioural and structural modifications. The latter usually feed more and excrete more than when untended, and hold aloft the honeydew droplets, often by means of specialised perianal hairs, rather than ejecting them some distance from the body. Appendages (cauda, siphunculi, legs) are commonly reduced, as is wax body-covering.

Considerable benefit accrues to the tended population. An increase in size, growth rate and fecundity are presumably the result of increased feeding, improved sanitation (by removal of pollutive excreta), reduced attack from natural enemies, and other protection provided. An ant-tended colony may thus thrive.

Ant-Hemiptera mutualism is very common in Australia, but has been little studied. [Way 1963; E. O. Wilson 1971; Stradling 1987]

Natural Enemies. In addition to vertebrate predators, which are most commonly lizards and birds, Hemiptera are attacked by many, diverse insect and arachnid predators and insect parasites, nematodes and fungal and other pathogens. Hymenopterous parasites of hemipterous eggs include many Scelionidae and many chalcidoids, especially Trichogrammatidae, Mymaridae, Encyrtidae, Eulophidae and Elasmidae. The sedentary, soft-bodied, aggregative, nymphal and adult Sternorrhyncha make easy and plentiful hosts. Aphelinidae parasitise Coccoidea, Aleyrodidae and Aphididae; many Encyrtidae parasitise Coccoidea and Psylloidea; Pteromalidae attack Coccoidea; the Aphidiinae (Braconidae) are obligatory parasites of Aphididae. Dryinidae are familiar ectoparasites of Cicadelloidea and Fulgoroidea (Fig. 3.28). Various Braconidae parasitise Heteroptera. Among the Lepidoptera, Cyclotornidae are ectoparasitic on ant-attended Eurymelidae and Psylloidea, and Epipyropidae on Fulgoroidea. Strepsiptera parasitise many Auchenorrhyncha and some Pentatomoidea (Figs 36.7A-C). Of the Diptera, Tachinidae frequently parasitise Lygaeidae, Coreidae and Pentatomoidea; Pipunculidae are endoparasitic in Cicadomorpha (except Cicadoidea) and Cecidomyiidae (6 spp. world-wide) in Psyllidae, Aphididae and Tingidae. Nematodes have been recorded as parasites of aquatic bugs. Fungal pathogens are sometimes common under humid conditions. Predators of eggs include other Hemiptera (Anthocoridae, phylinae Miridae, geocorine Lygaeidae) and predacious mites. The chief predators of nymphs and adults are Coleoptera and other Hemiptera (Anthocoridae, Nabidae, Reduviidae, *Asopus* group of Pentatomidae). Aphidoidea, Coccoidea and Psylloidea are particularly prone to attack by Coccinellidae (Coleoptera), Chrysopidae and Hemerobiidae (Neuroptera) and larvae of Syrphidae, Chamaemyiidae and Cecidomyiidae (Diptera).

Caterpillars of some Cosmopterigidae, Stathmopodinae, Pyralidae and Noctuidae are predatory on Coccoidea. Some sphecoid wasps (Gorytini, Stizini, Pemphredoninae, a few Crabroninae) provision their nests with Hemiptera. The impact of very generalised predators such as carabids, staphylinids and spiders is unknown.

Economic Significance. Many Hemiptera, both native and introduced, are pests of crop plants, all parts of which are attacked. The damage caused is often less apparent than that caused by mandibulate insects. Loss of sap results in stunting, distortion or wilting, especially when large populations of phloem-feeders, such as aphids, occur on young shoots. Intra-host feeding has made possible the efficient transmission of plant virus and other diseases, especially by aphids. Parenchyma-feeders among Miridae, Tingidae and Coreidae inject toxic saliva causing leaf necrosis, and mediate entry to pathogenic fungi. Many lygaeid seed-suckers similarly destroy seeds. Many Coreoidea, Lygaeidae and Pentatomidae suck fruits. The presence of only a few scale insects can make fruit unmarketable. Leaves and fruit may be soiled by sooty mould growing on honeydew, particularly of coccoids. Pyrrhocorid and lygaeid cotton stainers stain and damage cotton fibres. Some Cicadomorpha damage trees and shrubs, slitting the stems for oviposition. Corixidae and Notonectidae feed on fish eggs and fish fry. Triatomine reduviids transmit trypanosomiasis in tropical America; but the only obligate blood-sucker of humans in Australia is *Cimex lectularius*, which is not a proven vector of any disease. Some reduviids and the anthocorid *Lyctocoris campestris* occasionally 'bite' people, cattle and horses. Biological control has been successfully applied in Australia against the exotic aleyrodid *Trialeurodes vaporariorum* using an aphelinid parasite, the diaspidid *Aonidiella aurantii* and other coccoid pests (using Aphelinidae, Encyrtidae, Pteromalidae, Eulophidae), several aphid pests (Aphidiinae, *Aphelinus*) and the pentatomid *Nezara viridula* (using a scelionid).

On the other hand, predacious Heteroptera play an important part in regulating the populations of pest arthropods. Thus, many anthocorids, nabids, mirids and reduviids prey on eggs of phytophagous insects and tetranychid mites, and notonectids help control mosquito larvae. Hemiptera have been imported for the biological control of the exotic weeds, lantana (Tingidae), prickly pear (Coreidae and Dactylopiidae), Harrisia cactus (Pseudococcidae) and St John's wort (Aphididae). A mirid and an eriococcid have been exported to control, respectively, the sugarcane planthopper and manuka weed, both pests of Australian origin. Some Hemiptera or their products are sometimes used as human food e.g. honeydew, corixid eggs in Mexico, pentatomids (usually roasted) in parts of New Guinea and belostomatid 'sauce' in Thailand and Vietnam. Cochineal and kermes dyes and natural shellac are derived from coccoids.

Special Features of the Australian Fauna

The largest taxa are the Coccoidea, Cicadelloidea, Miridae, Fulgoroidea, Lygaeidae, Pentatomidae, Psyllidae and Reduviidae.

Notable deficiencies are native Aphidoidea; instead, the continent features a rich fauna of Coccoidea and Psylloidea highly adapted to the dry, sclerophytic environment. Though spittle bugs (Cercopidae and Aphrophoridae) are well represented in South-East Asia, only 21 spp. are known from Australia. The blood-sucking Cimicidae, Polyctenidae and triatomine Reduviidae are very poorly represented.

The small families, Hyocephalidae and Lestoniidae, are endemic. Cicadidae are highly endemic; 98% of the species and 72% of the genera are restricted to Australia. The primitive cicada family Tettigarctidae is known from one extant Australian genus and fossil genera in the Mesozoic of the Northern Hemisphere.

Relictual Gondwanan elements in the hemipterous fauna are characterised by primitive morphological features and host associations, disjunct distributions (especially in closed, montane rainforests) and by being related to taxa in other Gondwanan fragments, especially South America. The most notable example is the Peloridiidae. Other Gondwanan elements include the aphids *Neophyllaphis* (on the southern conifers *Podocarpus* and *Araucaria*) and *Taiwanaphis* (on antarctic beech, *Nothofagus*); Cephalelini (Cicadellidae) on Restionaceae; Aenictopecheidae; Thaumastocoridae; *Diaprepocoris* (Corixidae); Isoderminae (Aradidae); *Tasmanicola* (Lygaeidae); Idiostolidae; the flightless *Myerslopella* (Cicadellidae), *Notuchus* (Delphacidae), *Kumaressa* (Aradidae) and some coleopteriform Cylapinae (Miridae); and the flightless, terrestrial *Austrovelia* (Mesoveliidae). Australian Cleradini (Lygaeidae) are mostly endemic, the 22 species representing half the world total; in Australia, as far as is known, they are haematophages of possums (Phalangerioidea), an association strongly suggestive of a Gondwanan origin.

Autochthonous (Australian) elements comprise those taxa derived from the Gondwanan biota which underwent considerable diversification in adaptation to the changing climate (especially increased aridity) and diversifying, autochthonous, scleromorphic flora (e.g. *Eucalyptus*, *Acacia*, *Casuarina*) of the rafting, isolated continent. Psylloidea and Coccoidea provide the most spectacular examples, e.g. the lerp-producing spondylaspidine Psyllidae on *Eucalyptus*, and the gall-producing apiomorphine Eriococcidae. Other autochthonous elements include the many endemic Eurymelidae, Cicadellidae, Cicadidae, Amorbinini (Coreidae) and *Halys* group (Pentatomidae) host-specific to *Eucalyptus*.

The Northern (Indo-Malayan) elements, comprising those taxa resulting from Australia's recent connection with South-East Asia, are largely confined to tropical Australia, colonise plant hosts of recent origin, and are related to Asian taxa. Many of the Hemiptera of the eastern, non-montane areas of the Torresian zone can be placed in this category. Examples include many Fulgoroidea, Nirvaninae, Cicadellinae (Cicadellidae), Heterogastrinae (Lygaeidae) and Tessaratomidae.

The partial, physical isolation of the south-western region of the Bassian zone from its eastern counterpart is reflected in high endemism, e.g. in the Lygaeidae.

CLASSIFICATION

Order HEMIPTERA
(5650 Australian spp.)

Suborder STERNORRHYNCHA (1413)

PSYLLOIDEA (379)

1. Psyllidae (330)
2. Calophyidae (3)
3. Phacopterionidae (3)
4. Homotomidae (3)
5. Carsidaridae (4)
6. Triozidae (36)

ALEYRODOIDEA (31)

7. Aleyrodidae (31)

APHIDOIDEA (163)

8. Aphididae (157)

9. Adelgidae (3)
10. Phylloxeridae (3)

COCCOIDEA (840)

11. Margarodidae (40)
12. Ortheziidae (3)
- Phenacoleachiidae (0)
13. Pseudococcidae (240)
14. Eriococcidae (172)
15. Dactylopiidae (5)
- Kermesidae (0)
- Aclerididae (0)

- Stictococcidae (0)
16. Asterolecaniidae (25)
17. Cerococcidae (5)
18. Lecanodiaspididae (22)
19. Coccidae (78)
20. Kerriidae (7)
- Phoenicococcidae (0)
21. Conchaspidae (1)
- Beesoniidae (0)
22. Halimococcidae (2)
23. Diaspididae (240)

Suborder AUCHENORRHYNCHA (1532)

Cicadomorpha

CICADOIDEA (252)

24. Tettigarctidae (2)
25. Cicadidae (250)

CERCOPOIDEA (31)

26. Cercopidae (9)
27. Aphrophoridae (12)
28. Machaerotidae (10)
- Clastopteridae (0)

CICADELLOIDEA (813)

- Aetalionidae (0)
29. Cicadellidae (664)

Hylicidae (0)

30. Eurymelidae (92)
31. Membracidae (57)

Fulgoromorpha

FULGOROIDEA (436)

32. Delphacidae (64)
33. Cixiidae (42)
34. Meenoplidae (10)
35. Fulgoridae (21)
36. Achilidae (24)
37. Derbidae (49)
38. Dictyopharidae (10)

- Achilixiidae (0)
- Kinnaridae (0)
- Tettigometridae (0)
39. Tropiduchidae (7)
- Acanaloniidae (0)
40. Issidae (29)
41. Flatidae (96)
42. Nogodinidae (8)
43. Eurybrachyidae (44)
44. Lophopidae (3)
45. Ricaniidae (29)
- Gengidae (0)
- Hypochthonellidae (0)

Suborder HETEROPTERA (2705)

Coleorrhyncha

PELORIDIOIDEA (5)

46. Peloriidae (5)

Enicocephalomorpha

ENICOCEPHALOIDEA (30)

47. Enicocephalidae (28)
48. Aenictopecheidae (2)

Dipsocoromorpha

DIPSOCOROIDEA (88)

49. Ceratocombidae (4)
50. Dipsocoridae (24)
- Hysipterygidae (0)
51. Schizopteridae (60)
- Stemmocryptidae (0)

Gerromorpha

MESOVELIOIDEA (4)

52. Mesoveliidae (4)

HEBROIDEA (7)

53. Hebridae (7)

HYDROMETROIDEA (8)

- Paraphrynoveiliidae (0)
- Macroveliidae (0)
54. Hydrometridae (8)

GERROIDEA (74)

55. Hermatobatidae (3)
56. Veliidae (39)
57. Gerridae (32)

Leptopodomorpha

LEPTOPODOIDEA (3)

58. Leptopodidae (2)
59. Omaniidae (1)

SALDOIDEA (16)

- Aepophilidae (0)
60. Saldidae (16)

Nepomorpha

NEPOIDEA (14)

61. Nepidae (10)
62. Belostomatidae (4)

OCHTEROIDEA (31)

63. Ochteridae (8)
64. Gelastocoridae (23)

CORIXOIDEA (31)

65. Corixidae (31)

NAUCOROIDEA (8)

66. Naucoridae (8)

NOTONECTOIDEA (44)

67. Notonectidae (40)
68. Pleidae (4)
- Helotrephidae (0)

Cimicomorpha

CIMICOIDEA (47)

69. Anthocoridae (24)
70. Cimicidae (1)
71. Polycetenidae (2)
- Plokiophilidae (0)
- Medocostidae (0)

- Velocipedidae (0)
72. Nabidae (20)
- MIROIDEA (600)
73. Miridae (600)
- Microphysidae (0)
- TINGOIDEA (148)
- Vianaididae (0)
74. Tingidae (148)
- Joppeicidae (0)
- THAUMASTOCOROIDEA (11)
75. Thaumastocoridae (11)
- REDUVIOIDEA (300)
- Pachynomidae (0)
76. Reduviidae (300)

Pentatomomorpha

ARADOIDEA (176)

77. Aradidae (175)
78. Termitaphididae (1)

IDIOSTOLOIDEA (3)

79. Idiostolidae (3)

PIESMATOIDEA (4)

80. Piesmatidae (4)

LYGAEOIDEA (428)

81. Colobathristidae (1)
- Malcidae (0)
82. Berytidae (7)
83. Lygaeidae (401)
84. Largidae (7)
85. Pyrrhocoridae (12)

COREOIDEA (76)

- 86. Stenocephalidae (2)
- 87. Hyocephalidae (2)
- 88. Coreidae (57)
- 89. Alydidae (9)
- 90. Rhopalidae (6)

PENTATOMOIDEA (549)

- 91. Urostylidae (1)
- 92. Plataspididae (16)
- Thyreocoridae (0)
- Megarididae (0)
- Canopidae (0)
- Phloeidae (0)
- Thaumastellidae (0)

- 93. Cydnidae (43)
- 94. Acanthosomatidae (52)
- 95. Lestoniidae (2)
- 96. Tessaratomidae (15)
- 97. Scutelleridae (26)
- 98. Dinidoridae (3)
- 99. Pentatomidae (391)

The classification of the Hemiptera into the suborders Homoptera and Heteroptera is not followed here. The paraphyletic nature of the Homoptera is now widely acknowledged. Accordingly, the Homoptera are here represented by two suborders, Sternorrhyncha and Auchenorrhyncha, so that, with the Heteroptera, three suborders are recognised (Fig. 30.14). The Sternorrhyncha are shown as the sister group of the rest of the Hemiptera, a grouping supported by Kristensen (1975), Hennig (1981), Popov (1981), Wootton and Betts (1986) and the authors, but not by Hamilton (1981).

The Coleorrhyncha are no longer considered to

belong with the Sternorrhyncha and Auchenorrhyncha. Schlee (1969) determined them as the sister group of the Heteroptera and designated (Coleorrhyncha + Heteroptera) as the Heteropteroidea. Here, they have been returned to the Heteroptera as the sister group of the rest of the Heteroptera.

The arrangement into infraordinal (-morpha) groups is based on the cladistic analyses of Štys and Kerzhner (1975), N. M. Andersen (1982) and Schuh (1986a) and must be considered tentative in part. It does show clearly the inadequacy of the earlier division of the Heteroptera into Amphibicorisae, Hydrocorisae and Geocorisae.

Key to the Superfamilies of Hemiptera Known in Australia
(Adults only but including immature Aleyrodoidea and Psylloidea)

1. Antennal flagellum in form of an annulate or segmented arista (Fig. 30.31A), pedicel may be heavily sensoriated (Fulgoroidea) (Fig. 30.37F); hind tibiae and tarsi with saltatorial spines, often with pecten at apices of tibiae and tarsi, and spines on tibial shaft (Figs 30.31B–D, 37A–E); wing venation usually well developed (Figs 30.4E–H, 5A); phytophagous AUCHENORRHYNCHA. 11
- Antennal flagellum not aristoid, pedicel never heavily sensoriated; spines, if present on hind tibiae and tarsi, predominantly apical (Psylloidea) or predominantly on tibial shaft (e.g. Cydnidae) or insects parasitic or aquatic; wing venation simple or reduced 2
- 2(1). Insertion of labium remote from prosternum (Figs 30.1C, D); fore wings, if present and fully developed, usually held flat over abdomen when at rest, with apices widely overlapping (Fig. 30.47); often in the form of hemelytra, with a basal, sclerotised corium and an apical membrane (Figs 30.62A, 72); sometimes hyaline, with raised, reticulate venation (Figs 30.46, 61); sometimes elytriform (Fig. 30.53C); vannus and vannal fold present in hind wing (Figs 30.5B–D); scent glands usually present, and usually opening ventrolaterally on metathorax (Figs 30.3, 7A); antennae maximally 5-segmented, tarsi maximally 3-segmented; predacious and aquatic groups common, with legs adapted for predation and swimming HETEROPTERA. 14
- Insertion of labium near to or between prosternum (Figs 30.18, 19, 21–24); mouth-parts may be absent or vestigial (some Coccoidea, Aphidoidea); fore wings, if present, fully developed, usually held roof-wise, never truly flat, over abdomen, never strongly overlapping, of uniform texture, without sharp differentiation into a coriaceous base and a membranous apical area; not with raised, reticulate venation; never elytriform (Figs 30.4A–D); vannus and vannal fold absent from hind wing (Fig. 30.4D); antennae maximally 16-segmented; tarsi maximally 2-segmented; very rarely predacious or aquatic STERNORRHYNCHA. 3
- 3(2). Labium present 4
- Labium absent (Fig. 30.22C) 10
- 4(3). Wings present 5
- Wings absent 7
- 5(4). Antennae 3–6-segmented, the apical segment usually differentiated into a more slender terminal part (processus terminalis); basal tarsal segment small; pair of dorsolateral abdominal pores or tubules (siphunculi) usually present; fore wing with composite vein parallel to costal margin, ending in a pterostigma; RP usually arched; M and Cu obliquely oriented; hind wing usually with 1 longitudinal and 2 oblique veins (Fig. 30.4D); 3 ocelli present APHIDOIDEA (pt, p. 452)
- Antennae 7–10-segmented, with 1–2 apical setae; tarsal segments subequal in size; siphunculi absent; wing venation not as above; 2 or 3 ocelli present 6
- 6(5). Fore wings of harder consistency than hind wings; both M and Cu usually branching once, peripheral veins and clavus present (Figs 30.4A, B); antennae usually 10-segmented; 3 ocelli present; without vasiform orifice or large paired, ventral abdominal wax glands; body not wax dusted (Fig. 30.15) PSYLLOIDEA (pt, adults; p. 448)
- Fore wings membranous with reduced venation (Fig. 30.4C); antennae 7-segmented; 2 ocelli present; abdomen dorso-subapically with vasiform orifice (Fig. 30.17E) and usually with pairs of large wax glands on some sternites; body, including wings, often completely wax-dusted (Fig. 30.17F) ALEYRODOIDEA (pt, adults; p. 450)

- 7(4). Legs and antennae present; tarsi usually bearing 2 claws; with compound eyes or 3-lensed eyes or both 8
Legs and antennae present or absent; tarsi 1-clawed or absent; eyes 1- or 2-lensed, or absent 9
- 8(7). Antennae 1–6-segmented, the apical segment usually differentiated apically into a more slender part (processus terminalis); tarsi usually 2-segmented, the basal segment small; with 2 empodial hairs; paired siphunculi, varying from pores to tubules, commonly present dorsolaterally on abdomen; eyes either compound, each with a 3-lensed ocular tubercle (triommatidion) appended to posterior margin, or triommatidia only present; circumanal pore rings absent (Figs 30.18, 19) APHIDOIDEA (pt, apterous adults; p. 452)
- Antennae 1–10-segmented, processus terminalis absent; tarsi fused with tibiae or 1-segmented, and each often with a well-developed arolium; eyes compound; circumanal pore ring(s) present; may be protected by a test or 'lerp' (Figs 30.15, 16A–D) PSYLLOIDEA (pt, nymphs; p. 448)
- 9(7). An operculated anal fossa (vasiform orifice) present dorso-subapically on body; body sessile, scale- or casket-like, often wax-producing, legs and antennae reduced (Figs 30.17C–F) ALEYRODOIDEA (pt, nymphs of instars II–IV, puparia; p. 450)
- Vasiform orifice absent, though other perianal apparatus may be present; body may be coccoid, scale-like, wax- or scale-producing, gall-forming; legs and antennae often reduced and sessile (Figs 30.21–25) COCCOIDEA (pt, ♀ ♀; p. 457)

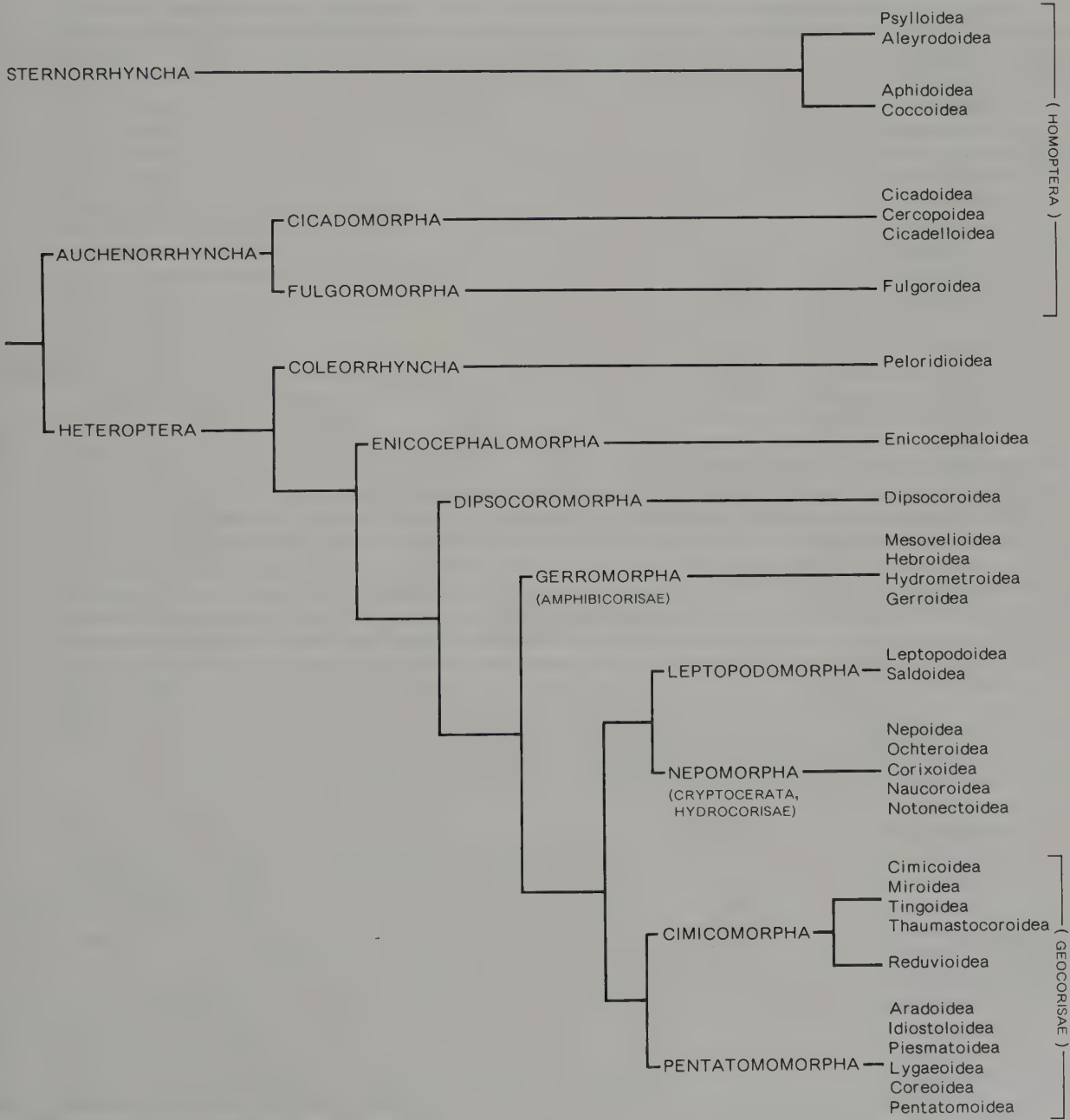


Fig. 30.14 Classification of the Hemiptera.

- 10(3). Tarsi 1-clawed; alate ♂♂ with hind wings reduced to hamulohalteres (Fig. 30.25A), or apterous ♂♂ or ♀♀ COCCOIDEA (pt, ♂♂, some ♀♀; p. 457)
 Tarsi usually 2-clawed; apterous APHIDOIDEA (pt, some sexuales; p. 452)
- 11(1). Tegulae almost always present on mesothorax; mid coxae elongate, widely separated; antennae ventral to eyes; pedicel enlarged, often bulbous, with numerous wart-like sensilla (Fig. 30.37) FULGOROIDEA (p. 474)
 Tegulae absent; mid coxae short, not widely separated; antennae anterior to eyes; pedicel not or scarcely thicker than scape, without wart-like sensilla 12
- 12(11). Head with 3 ocelli on crown; fore femora thickened (Figs 30.26, 27) CICADOIDEA (p. 465)
 Head with 2 ocelli; these variable in position, or absent; fore femora not thickened 13
- 13(12). Hind tibiae short, cylindrical, with 1 or 2 strong, lateral spines and flared apical pecten; hind coxae conical (Fig. 30.30) CERCOPOIDEA (p. 467)
 Hind tibiae long, angular, with a few, or, more usually, numerous lateral spines, often in conspicuous rows; apical pecten narrow, composed of macrosetae; hind coxae transverse, plate-like (Figs 30.31–34) CICADELLOIDEA (p. 468)
- 14(2). Antennae shorter than head, entirely concealed beneath head, or scarcely visible dorsally; underwater, near water, in moss or associated with termites 15
 Antennae as long as or longer than head, exposed and fully visible from above; never completely aquatic 22
- 15(14). Head very transverse, produced interocularly and anteriorly to form laminate expansion, which usually bears 2 or more hyaline, membranous areolae; opisthognathous; pronotum produced laterally to form laminate paranota containing similar areolae; fore wings hyaline, with many areolae bordered by raised veins (Fig. 30.46); eyes often subpedunculate; antennae 3-segmented (New Caledonian species without areolae) PELORIDIOIDEA (p. 479)
 Without such a combination of characters 16
- 16(15). Body flat, ovoid, with lateral lamellae bearing, marginally, numerous lanceolate processes; without eyes or wings (Fig. 30.66); associated with termites ARADOIDEA (pt, Termitaphididae, p. 496)
 Body never with such marginal lamellae and processes; eyes present, wings present or absent; mostly aquatic, sometimes near water 17
- 17(16). Ocelli present; living on shores or banks (Fig. 30.56) OCHTEROIDEA (p. 487)
 Ocelli absent (except in *Diaprepocoris* (Corixidae) which has palae and other corixid characters as in couplet 18); aquatic, except on dispersal flights 18
- 18(17). Fore tarsi usually scoop-like (palae), with a row of long hairs, never with 2 claws (Fig. 30.57); head slightly overlapping pronotum; dorsum never strongly arched CORIXOIDEA (p. 488)
 Fore tarsi not scoop-like, sometimes with 2 claws; head set normally in prothorax; dorsum of body may be longitudinally strongly arched 19
- 19(18). Apex of abdomen with a cylindrical respiratory siphon composed of 2 filaments usually about as long as body (Figs 30.54A, B) NEPOIDEA (pt, Nepidae, p. 486)
 Respiratory siphon short and flat, or absent 20
- 20(19). Fore legs raptorial, with femur greatly thickened; dorsum not unusually convex 21
 Fore legs not raptorial; dorsum very strongly convex above (Figs 30.57C, D) NOTONECTOIDEA (p. 488)
- 21(20). Membrane of hemelytron with veins; apex of abdomen with 2 short, flat respiratory filaments (Fig. 30.55); mid and hind tibiae with well-developed fringes of long, swimming hairs NEPOIDEA (pt, Belostomatidae, p. 486)
 Membrane of hemelytron, if developed, without veins; abdomen without respiratory filaments (Figs 30.54C, D); mid and hind tibiae spinose, swimming hairs variously developed NAUCOROIDEA (p. 488)
- 22(14). Pronotum entirely or almost covering scutellum; ocelli absent; tarsi 2-segmented; fore wings not differentiated into corium and membrane, with a raised, lace-like reticulation enclosing small cells (Fig. 30.61); body less than 5 mm long TINGOIDEA (p. 493)
 Pronotum usually not covering scutellum, but if so, then ocelli present and/or tarsi 3-segmented; fore wings usually with corium and membrane, and without a lace-like reticulation; size varied 23
- 23(22). Flightless ectoparasites of mammals and birds; fore wings represented by short, coriaceous scales; at least head and pronotum much flattened; ocelli and sometimes eyes absent (Figs 3.25B, 30.58A) CIMICOIDEA (pt, Cimicidae, Polycetenidae, p. 489)
 If flightless, not ectoparasites with above form; ocelli present or absent; eyes always present 24
- 24(23). Tarsal formula usually 1:2:2; fore legs raptorial, with short, squat tarsus and apically expanded tibia; fore wings entirely membranous; head constricted, then globularly swollen behind eyes; pronotum commonly twice transversely constricted (Fig. 30.47) ENICOCEPHALOIDEA (p. 480)
 Tarsal formula 3:3:3 (Fig. 30.73) or 2:2:2 (Fig. 30.68) (in some non-Australian spp. 1:1:1); fore legs not so disposed; fore wings uniformly textured or with a corium; head and pronotum not so constricted 25
- 25(24). Tarsi 2-segmented, very small, much more slender than tibiae; tibiae with apical process almost as long as tarsi; body flattened dorsoventrally (Fig. 30.58E) THAUMASTOCOROIDEA (p. 494)
 Tarsi often 3-segmented, if 2-segmented, robust, not slender as above; tibiae without apical process; body form varied 26
- 26(25). Body length less than 4 mm; ocelli usually present; antennae 4-segmented, segments 3 and 4 bristly, each longer and more slender than segments 1 or 2; segment 3 slightly swollen at base (Fig. 30.48) DIPSOCOROIDEA (p. 481)
 Body length usually more than 4 mm, but if less, and 3rd and 4th antennal segments slender, then ocelli absent and/or

- p. 27
-
- antennae with either 1st or 2nd segment as long as or longer than 3rd or 4th 27
-
- 27(26). Apex of head ventrally produced, so that base of labium permanently distant from underside of head (Fig. 30.53B);
-
- ocelli between eyes and distant from their posterior margins; eyes large and prominent (Figs 30.52, 53); living near
-
- water (sometimes intertidal) or in wet places 28
-
- Apex of head not ventrally produced, labium usually either straight and in repose lying closely parallel to head and
-
- thorax (Figs 30.1C, D) or permanently curved and thus distant from underside of head (Figs 30.62–64); if labium
-
- distant from head, ocelli behind or near level of posterior margins of eyes or absent and/or eyes not large and
-
- prominent; habits varied 29
-
- 28(27). Apical area of fore wing with open cells or fore wings elytriform; labium basally, and fore femora sometimes, with
-
- long spines LEPTOPODOIDEA (p. 485)
-
- Membrane of fore wing with 4 closed cells; labium and fore femora without long spines SALDOIDEA (p. 485)
-
- 29(27). Head several times longer than wide, narrow, but somewhat dilated in front, with eyes about half way along its length
-
- (Fig. 30.49A) HYDROMETROIDEA (p. 482)
-
- Head no more than about twice longer than wide, not dilated in front, with eyes at or near base 30
-
- 30(29). Claws of at least fore legs inserted well before apex of ultimate tarsal segment (Figs 30.50D, 51C)
-
- GERROIDEA (p. 483)
-
- Claws of all legs apical..... 31
-
- 31(30). When winged, body flattened dorsoventrally and sides of abdomen extending well beyond hemelytra; apterous spp.
-
- usually not flattened; ocelli absent; antennae with 4 segments usually of similar diameter; tarsi 2-segmented (Fig.
-
- 30.65); often on or under bark ARADOIDEA (pt, Aradidae, p. 496)
-
- Body rarely much flattened or with sides of abdomen extending well beyond hemelytra; if ocelli absent, antennae with
-
- segments not all of similar diameter and/or tarsi 3-segmented 32
-
- 32(31). Tarsi with basal segment minute, several times shorter than 2nd; pronotum and corium without deep punctures; fore
-
- wing without costal fracture; membrane, when present, without veins (Fig. 30.49B); on surface or near edge of
-
- water, or in wet places 33
-
- Tarsi with basal segment usually as long as or longer than 2nd, if much shorter, then pronotum and corium with deep
-
- punctures (Piesmatidae, Fig. 30.68) or costal fracture present or membrane with veins; terrestrial 34
-
- 33(32). Tarsi 2-segmented; small bugs 2 mm or less in length; prominent bucculae extend length of head, flanking labium in
-
- deep sulcus (Fig. 30.49B) HEBROIDEA (p. 482)
-
- Tarsi 3-segmented; elongate oval bugs over 2 mm in length; without bucculae and sulcus (Fig. 30.49C)
-
- MESOVELIOIDEA (p. 482)
-
- 34(32). Scutellum reaching apex of clavus or beyond, sometimes covering abdomen (Figs 30.79B, C, 80–82); if not then claval
-
- commissure very short (Fig. 30.79A); wings always present; antennae usually 5-, sometimes 3- or 4-segmented
-
- PENTATOMOIDEA (p. 504)
-
- Scutellum not reaching apex of clavus (e.g. Figs 30.58, 73, 77); wings present or absent; antennae 4-segmented 35
-
- 35(34). Hemelytral membrane usually with no more than 3 longitudinal veins sometimes enclosing cells (Fig. 30.59); if
-
- (rarely) membrane with more than 3 veins (Figs 30.58C, D) or membrane (or entire hemelytron) absent, apex of fore
-
- and mid tibiae with a large pad, or base of labium curved and well separated from underside of head, even in repose
-
- (Fig. 30.62); abdomen without ventral trichobothria 36
-
- Hemelytral membrane, when fully developed, usually with 4 or more longitudinal veins (Figs 30.78, 81A, C); if mem-
-
- brane reduced or absent or (rarely) with fewer than 4 veins, then apex of fore and mid tibiae without large pad, and
-
- base of labium straight (Figs 30.1C, D) so that in repose labium lies closely parallel to head and thorax; abdomen
-
- usually with ventral trichobothria (Figs 30.74, 76B, 77B) 38
-
- 36(35). Hemelytra, except in some brachypters, with a cuneus; membrane with 1 or usually 2 closed cells near cuneus (Figs
-
- 30.5C, 59); ocelli absent (except in Isometopinae, Fig. 30.58F) MIROIDEA (p. 491)
-
- Hemelytra usually without a cuneus; if cuneus present, membrane without closed cells and ocelli present 37
-
- 37(36). Prosternum usually with median stridulatory groove extending anterior to fore coxae (Fig. 30.8A); labium apparently
-
- 3-segmented and usually permanently curved and well separated from underside of head, even in repose (Figs
-
- 30.62–64); if labium straight, hemelytron with 2 or 3 large, very long closed cells occupying most of membrane (as
-
- in Fig. 30.62) REDUVIOIDEA (p. 494)
-
- Prosternum without a stridulatory groove; labium 4- or apparently 3-segmented, not permanently curved away from
-
- head; hemelytron usually without 2 or 3 closed cells occupying most of membrane, if with such cells, also with
-
- numerous longitudinal veins (Figs 30.58C, D), and labium obviously 4-segmented CIMICOIDEA (pt, p. 489)
-
- 38(35). Tarsi 2-segmented; body less than 5 mm long; pronotum and corium covered with deep punctures; hemelytra covering
-
- abdomen, with much reduced membrane; scutellum much shorter than claval commissure; tingid-like species on
-
- Acacia or Beyeria (Fig. 30.68) PIESMATOIDEA (p. 499)
-
- Tarsi usually 3-segmented; size, punctuation, hemelytra and habits varied, but if (rarely) less than 5 mm long, deeply
-
- punctate and with 2-segmented tarsi, then hemelytra either with large membrane, or staphyliniform and scutellum
-
- not shorter than clavus 39
-
- 39(38). Ocelli present (Fig. 30.73A) 40
-
- Ocelli absent (Figs 30.73B, C) LYGAEOIDEA (pt, p. 499)
-
- 40(39). Abdomen laterobasally with an ovoid pore-bearing plate on each side (Fig. 30.76B); opening of metapleural scent
-
- gland with bristle-like process (Fig. 30.76C) COREOIDEA (pt, Hyocephalidae, p. 503)

- Abdomen without such plates; opening of metapleural scent gland without a bristle-like process 41
- 41(40). Membrane of hemelytron in macropters with at least 6 and usually many more longitudinal veins (Figs. 30.67, 78); brachypters with antennifers usually inserted dorsolaterally, above the line between centre of eyes and clypeo-labral suture 42
- Membrane of hemelytron in macropters usually with fewer than 6 main longitudinal veins (Figs 30.70, 72); brachypters with antennifers inserted ventrolaterally, on or below the line between centre of eyes and clypeo-labral suture LYGAEOIDEA (pt, p. 499)
- 42(41). Macropterous; antennifers inserted ventrolaterally (Fig. 30.67); S6 with 4 short trichobothria on each side near spiracle IDIOSTOLOIDEA (p. 498)
- Macropterous or brachypterous; brachypters with antennifers inserted dorsolaterally; S6 with 3 or fewer trichobothria on each side (cf. Figs 30.76B, 77B) COREOIDEA (pt, p. 503)

Suborder STERNORRHYNCHA

The Sternorrhyncha comprise the psyllids or jumping plant lice, whiteflies, aphids, coccids, mealybugs and scale insects. All are phytophagous, mostly feeding in phloem of angiosperms but also some gymnosperms.

They are a monophyletic group and are the sister group of the rest of the Hemiptera. Their monophyly is established by the absence of a vannus and vannal fold in the hind wing, and the movement of the mouth-parts so far posteriorly that the labium originates from the prosternum. A gut filter system is usually present and may feature an encapsulating hind gut. Antennae are multisegmented and filiform. Tarsi are maximally 2-segmented.

The ground plan of the Hemiptera is characterised by small size; multisegmented, filiform antennae; large, bulbous clypeal region; homonomous wings, each with clavus, 2 anal veins and basally fused Sc+R+M, but without a hind wing vannus; saltatorial hind legs; 3-segmented tarsi; and, probably, the potential for parthenogenesis and alary polymorphism. The basal sternorrhynchous group (Psylloidea) is close to this ground plan, but the trend of the Sternorrhyncha has been towards smaller size, a reduction in morphological complexity (including wing venation), increased biological complexity, nymphal regression and sessility, and production of protective devices (scales, tests, gall initiation). The Auchenorrhyncha, on the other hand, have tended towards increased wing development and jumping capacity, and tymbal communication, while the Heteroptera have developed the hemelytron, prognathous head and complex scent gland systems.

Four monophyletic groups are contained within the Sternorrhyncha—Psylloidea, Aleyrodoidea, Aphidoidea and Coccoidea. The sister groups Psylloidea + Aleyrodoidea have in common many plesiomorphies, including excellent jumping capacity, and apomorphies such as pendunculate eggs. The sister groups Aphidoidea + Coccoidea are characterised by loss of jumping function of hind leg, presence of a composite, longitudinal vein in fore wing, reduction or loss of genitalia, 1st tarsal segment and pretarsus; and occurrence of viviparity and polymorphism. [Pesson 1951; Strümpel 1983]

Superfamily PSYLLOIDEA

by K. L. TAYLOR and M. CARVER

Jumping plant lice, lerp insects. All currently recognised families of Psylloidea (White and Hodkinson 1985; Burckhardt 1987–88) are represented in Australia. Most

Australian species belong to two subfamilies of Psyllidae, namely the predominantly Australian Spondylaspidinae, which are largely associated with *Eucalyptus*, and the Acizzinae, most Australian species of which colonise *Acacia*. The cosmopolitan Trioziidae are also well represented. The few Australian Calophyidae, Phacopterionidae, Homotomidae and Carsidaridae have Indo-Malayan affinities.

Psylloidea are more abundant and diverse in Australia than in the Northern Hemisphere. Most Australian species are endemic and associated with endemic hosts. Nymphs are usually confined to one host species or to a group of closely related species. Adults are less discriminating, and sometimes feed and oviposit on plants which do not support their nymphs. Adults and nymphs feed in phloem by way of the stomata (L. R. Clark 1962; Woodburn and Lewis 1973).

Adult (Fig. 30.15A) small. Genal processes commonly developed. Antennae 10-segmented. Ocelli 3. Stylets lodged in internal crumena. Hind legs saltatorial; coxae large, fixed; trochanters condylated; saltatorial spines at apices of tibia and 1st tarsal segment. R, M and Cu of fore wing each usually single branched; peripheral vein present; clavus present (Figs 30.4A, B). Proctiger well developed; circumanal wax gland ring(s) usually present in female. Sexes similar. Reproduction bisexual.

Nymphs (Fig. 30.15B) non-saltatorial; dorsoventrally flattened; head and prothorax fused. Stylets at rest looped externally at base of labium. Fore wing pad often produced anteriorly as a humeral lobe. Tibia and tarsus fused in instars I–IV; tarsus 1-segmented in final instar (V); well-developed arolium usually present. Wax production common, secreted mostly from base of lanceolate setae or *sectasetae* on abdomen. Nymphs of many Spondylaspidinae build remarkable lerps (scales, tests) on eucalypts (Figs 30.15F–H, 16A–D). Lerps are formed largely from anal excreta (honeydew) and have a high carbohydrate content. They take various forms, such as simple, sugary cones (*Glycaspis*), univalves (*Hyalinaspis*), bivalves (*Australopsylla*) or intricately woven baskets and fans (*Cardiaspina*) (K. L. Taylor 1962; K. M. Moore 1970; Basden 1970; Gilby *et al.* 1976).

Eggs (Fig. 30.11A) pedunculate, like those of Aleyrodidae. Either the peduncle is inserted into the plant tissue, from which water is absorbed (T. C. R. White 1968) or the entire egg is embedded in the plant, according to the structure of the ovipositor.

Leaf pit galls and closed woody galls are a common

feature of the Triozidae, and some Psyllidae also form galls.

The nymphs of some *Glycaspis* (lerp-forming), and *Phellopsylla* and *Aconopsylla* (free-living), are attended by ants.

Massive outbreaks have been recorded in some species of *Cardiaspina* and *Glycaspis* (Spondyliaspidae), result-

ing in host debilitation and leaf necrosis (L. R. Clark 1964; K. M. Moore 1961b; T. C. R. White 1970). Species of *Ctenarytaina* and *Blastopsylla* (Spondyliaspidae) and *Acizzia* (Acizziinae) have been accidentally introduced into New Zealand, South Africa, California and Europe, presumably on imported *Eucalyptus* and *Acacia*. [Hodkinson 1974; Morgan 1984]

Key to the Families of Psylloidea Known in Australia

1. Vena spuria present in fore wing, continuous with M_{3+4} and meeting RP (Fig. 30.15C); male with conspicuous dorsal processes on subgenital plate **Carsidaridae**
Vena spuria absent; subgenital plate without dorsal processes 2
- 2(1). Fore wing veins R, M and CuA arising at or near same point; pterostigma and costal break absent (Fig. 30.4B) **Trioizidae**
Fore wing veins M and CuA with distinct common stem; pterostigma or costal break present or absent 3
- 3(2). Fore wing vein RP short, terminating close to RA and pterostigma; pair of prominent dorsal processes on metapostnotum; on *Ficus* **Homotomidae**
Fore wing RP long, terminating at or near to apex of wing; metanotum without prominent processes; on various hosts 4
- 4(3). Veins RP and M_{1+2} meeting at one point to give an X-formation **Phacopterionidae**
Fore wing not as above 5
- 5(4). Hind coxal spur (*meracanthus*), absent or small and blunt; male proctiger bipartite; anteorbital lobes (Fig. 30.15B) present or absent 6
Meracanthus present and apically pointed (Fig. 30.15E); male proctiger unipartite; anteorbital lobes absent 8
- 6(5). Anteorbital lobes absent; hind coxae weakly developed; fore wing vein CuA 2-branched, RP and M_{1+2} either partially fused or linked by cross-vein *r-m* **Psyllidae** (*Anomalopsylla*)
Anteorbital lobes usually present; hind coxae strongly developed; CuA once-branched, RP and M_{1+2} not linked 7
- 7(6). Meracanthus absent; male proctiger with short apical segment. Nymphs with distinct abdominal segments (Fig. 30.15D); abdominal lanceolate or sectasetae and circumanal pore rings absent **Psyllidae** (lerp-building SPONDYLIASPIDINAE)
Meracanthus, if present, small and rounded; male proctiger with apical segment at least half as long as basal segment. Nymphs with caudal plate (fused abdominal segments); lanceolate or sectasetae present marginally on abdomen; circumanal pore rings present **Psyllidae** (free-living SPONDYLIASPIDINAE)
- 8(5). Basal hind tarsal segment usually with 2 spines; if with one, then rhinaria absent from antennal segments 3, 5 and 7 **Psyllidae** (ACIZZIINAE *et al.*)
Basal hind tarsal segment either without spines; or with one spine (*Cecidopsylla*) in which case rhinaria present on antennal segments 3, 5 and 7 **Calophyidae**

1. Psyllidae. The SPONDYLIASPIDINAE (Figs 30.11A, 15A, B, D, F-H, 16A-D) include 10 genera of lerp-building species on *Eucalyptus* (K. M. Moore 1970; K. L. Taylor 1962). *Glycaspis* (140 spp.) is the largest genus. Some lerp-forming *Glycaspis* cause shallow pit galls; others (subgenus *Synglycaspis*) cause large vesiculate galls and plug the orifices with lerp substance; and some *Australopsylla* are protected by both lerps and leaf roll galls. Tarsal oscillation is common in lerp-inhabiting species (Carver 1987). The free-living species colonise shoots of *Eucalyptus* and related Myrtaceae (K. L. Taylor 1987a, b); *Ctenarytaina* has about 25 known species and nymphs of *Anoeconeossa* inhabit the empty lerps of other Spondyliaspidae.

Only 22 Australian species of ACIZZIINAE (Figs 30.4A, 15E) have been described, but many others are known. Most belong in *Acizzia* but were originally assigned to *Psylla*. Many species of *Acacia* are host to more than one species of *Acizzia*. Other hosts include *Dodonaea*, *Apophyllum*, *Hakea*, *Eremocitrus* and *Leptospermum*. New growth is preferred, but *A. acaciaedecurrentis* and others colonise twigs.

Other Australian members of the family include

Aconopsylla sterculiae (PAUROCEPHALINAE) on bark of *Brachychiton* (Sterculiaceae); and *Anomalopsylla* (RHINOCOLINAE) on *Geijera* (Rutaceae). Of the DIAPHORININAE, *Diaphorina* [= *Brachyopsylla*] occurs on *Conyza* (Asteraceae), and the exotic *Psyllopsis fraxinicola* on *Fraxinus* (Oleaceae) in Tas. The Neotropical *Heteropsylla cubana* (CIRIACREMINAE), a pest of the important forage tree leucaena (Mimosaceae), is widespread in the Pacific region, and reached Qld in 1986.

2. Calophyidae. *Calophya* is known from W.A. The two Australian species of *Cecidopsylla* form leaf pit galls: *C. paterae* on *Geijera* and *C. putealis* on *Banksia* (Proteaceae). The abdominal venter of the nymph of *C. putealis* is extruded to occupy the cavity of the gall.

3. Phacopterionidae. Species of the predominantly Indo-Malayan *Pseudophacopteron* have been collected in Qld rainforest.

4. Homotomidae. *Mycopsylla fici*, *My. proxima* and *Macrohomotoma* sp. on *Ficus* (Moraceae), are the only Australian representatives. *Mycopsylla* nymphs live beneath solidified latex resulting from feeding punctures.

5. Carsidaridae (Fig. 30.15C). *Mesohomotoma hibisci* on *Hibiscus* (Malvaceae) and *Protyora* (3 spp.) on

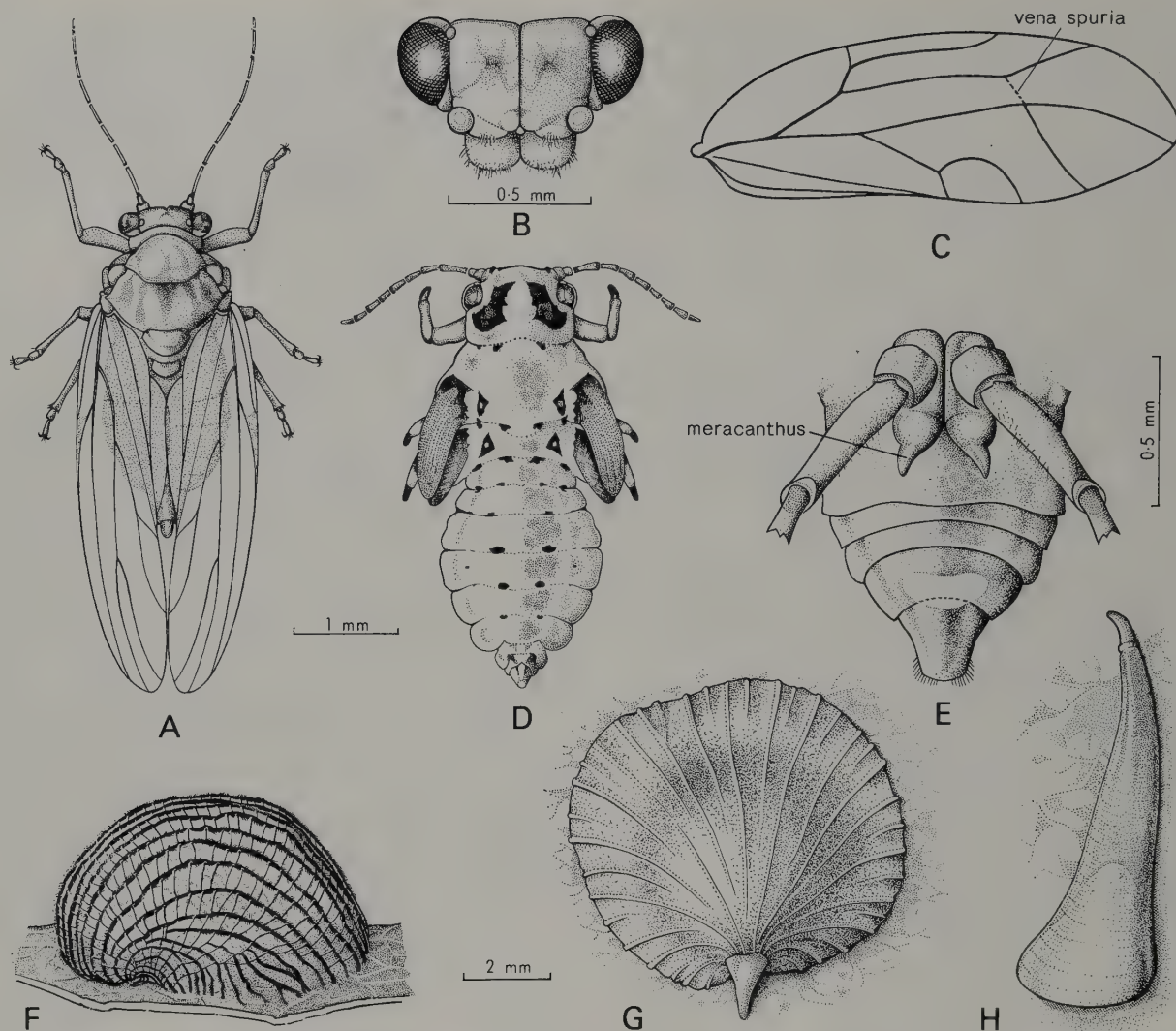


Fig. 30.15 Psylloidea: A, *Creiis costatus*, ♂; B, head of same; C, fore wing of *Protorya sterculiae*; D, 5th instar nymph of *Creiis costatus*; E, hind legs and abdomen of *Acizzia acaciaedecurrentis*, ventral; F, lerp of *Cardiaspina textrix*; G, lerp of *Creiis costatus*; H, lerp of *Creiis periculosa*. [T. Nolan]

Sterculiaceae are the only known Australian representatives. *P. sterculiae* (star psylla) aggregates on *Brachychiton* foliage; the nymphs bear long, waxy filaments at the apex of the abdomen. [Hollis 1987]

6. Triozidae (Fig. 30.4B). *Trioza* is a large, cosmopolitan genus. Only five Australian species are described, but many more await description. Hosts in Australia include Myrtaceae and Myoporaceae. Some species cause shallow leaf pit galls or leaf curling and distortion. *Schedotrioza* initiates formation of closed, globular, woody galls on *Eucalyptus* leaves (G. S. Taylor 1985). Two species of *Acanthocnema* occur on *Casuarina* (Casuarinaceae) and one on *Hakea* (Proteaceae). The nymph of *A. casuarinae* is elongate and flattened and lives, almost stationary, curved around a *Casuarina* leaf. *Leptynoptera sulfurea*, known from Darwin on *Calophyllum* (Guttiferae), is widespread in the Pacific. [Tuthill and Taylor 1955; Hollis 1984; Morgan 1984; Burckhardt 1987–88; Burckhardt and Lauterer 1989]

Superfamily ALEYRODOIDEA

by M. CARVER

7. Aleyrodidae (whiteflies) (Figs 30.4c, 16, 17). More than 1200 species of Aleyrodidae have been described, but only 31 species in 14 genera are recorded from Australia, and at least five of the species are exotic or have a cosmopolitan distribution. Undoubtedly, more species await collection, especially in the tropics. Morphologically and biologically, the adults resemble Psylloidea, whereas the immatures are more like Coccoidea. Adults are small (2 mm or less) and fragile, and usually evenly covered with white, waxy powder. Antennae 7-segmented, aphid-like; compound eyes usually either transversely constricted or completely separated into a dorsal and ventral component, each component sometimes with different-sized facets; 2 ocelli; 4-segmented rostrum, the 2nd segment retractable into the 1st; similar fore and hind wings, lying loosely flat over the abdomen,

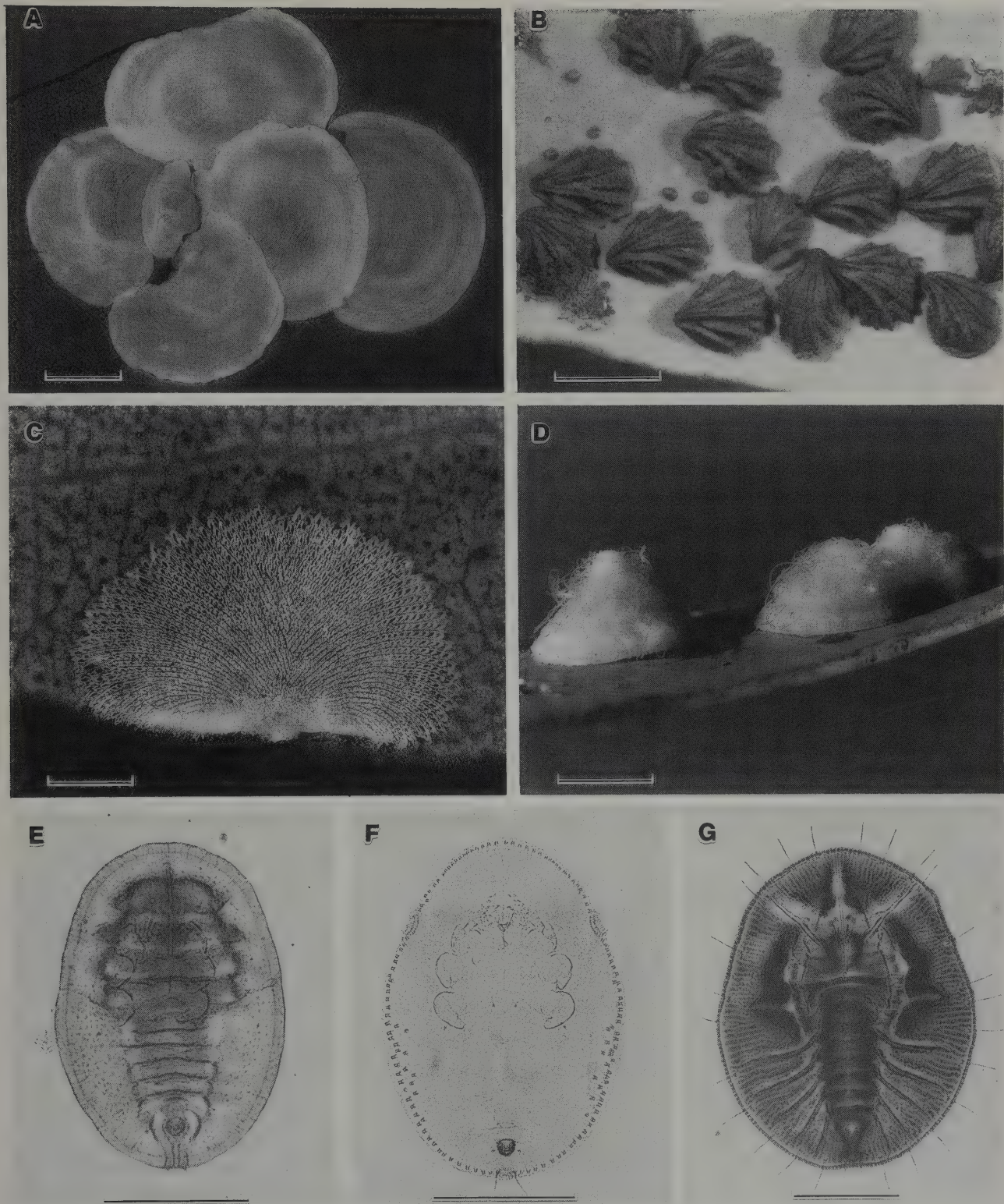


Fig. 30.16 A–D, lerps of spondyliaspine Psyllidae: A, *Lasiopsylla rotundipennis*; B, *Spondylaspis plicatuloides*; C, *Cardiaspina albitextura*; D, *Glycaspis* sp. E–G, puparia of Aleyrodidae: E, *Aleuroclava eucalypti*; F, *Orchamoplatus citri*; G, *Aleurocanthus* sp. Scale lines: A, B, D = 3 mm; C = 1 mm; E–G = 0.4 mm. [A. Edward, J. P. Green]

without coupling mechanism and with markedly reduced venation; 4 pairs of spiracles, 2 thoracic and 2 abdominal; tarsi of 2 equal segments, with 2 pretarsal claws and a

single setiform to pulvillar empodium; comb setae, especially on the hind tibiae, distribute waxy meal over the body from the abdominal venter, which bears large,

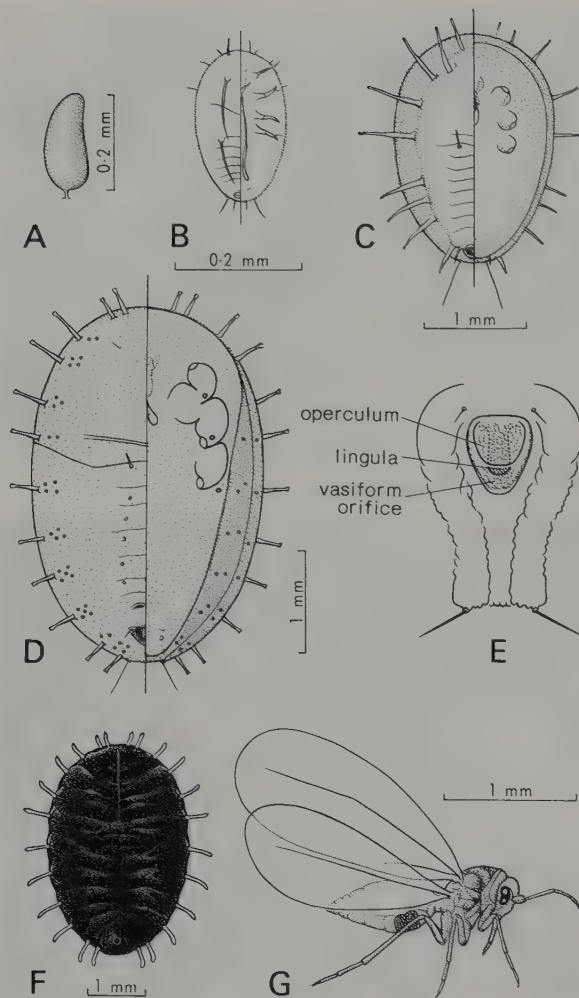


Fig. 30.17 Aleyrodidae: A–F, *Neomaskellia eucalypti*: A, egg; B, 1st instar (crawler); C, later instar; D, F, puparium; E, vasiform orifice; G, *Aleyrodidae* sp., adult ♀. [A–D, F, G by S. Monteith; E by S. P. Kim]

paired, segmentally arranged wax plates; well-developed genitalia comparable with those of Psylloidea (Weber 1935).

Unique to Aleyrodidae and present in all instars is the *vasiform orifice*, a deep, cup-like fold medially in T8, in which the anus opens between a tongue-shaped process (*lingula*) and a dorsal lid (*operculum*). The whole is a device to prevent excretal pollution; honeydew droplets which form are propelled from the body by the lingula in a manner similar to that of the aphid cauda.

Nymphs are scale-like and often wax-covered. The 1st instar is minute, has well-developed simple eyes, antennae and legs, and actively seeks and settles in a suitable permanent feeding place. In the later nymphal instars the appendages are atrophied. The 4th (final) instar nymph eventually ceases feeding and becomes a puparium; in some species such as *Trialeurodes vaporariorum* a vertical, waxy palisade is secreted between the margins of the dorsum and venter to form a coffin-like puparium. The adult emerges through an inverted T-shaped split in the dorsum.

The eggs are pedunculate, like those of Psylloidea. The

peduncle, a hollow extension of the chorion, is inserted into the host plant through a slit made by the ovipositor, or directly through a stoma. Water is thus absorbed from the host plant via the peduncle. The females of many species pivot on the inserted feeding stylets while ovipositing, thereby laying their eggs in an arc or circle. Arrhenotokous and thelytokous parthenogenesis is common and thelytokous races are known.

Aleyrodidae are less host-specific than Aphidoidea or Psylloidea. Hosts are almost exclusively angiosperms, mostly woody dicots. Such preference could be a reflection of their tropical distribution. World-wide, *Ficus* (Moraceae) is host to more than 80 species of Aleyrodidae, and *Citrus* (Rutaceae) to more than 60. However, among the well-known polyphagous species, *T. vaporariorum* (greenhouse whitefly), with hosts in more than 80 plant families, and *Bemisia tabaci*, show a preference for herbaceous dicots. Most Australian aleyrodids colonise Proteaceae, Epacridaceae, Myrtaceae and Mimosaceae. Exotic species include *T. vaporariorum*, *B. tabaci*, *Aleurodicus destructor*, *Dialeurodes kirkaldyi* and *Pealius azaleae*. *Neomaskellia bergii*, on sugar cane and other grasses in Australia and elsewhere, is one of few species world-wide known to be ant-attended.

Many Aleyrodidae have been reported as vectors of plant viruses, but only three species are proven vectors: *T. vaporariorum*, *T. abutilonea* (extra-Australian) and *B. tabaci* (Mound 1973). *T. vaporariorum* was for a long time considered to be under complete biological control by an introduced aphelinid parasite *Encarsia formosa*. *Orchamoplatus citri* and *Bemisia giffardi* are occasionally minor pests of citrus.

The taxonomy of the family is based on the sessile, more easily available 4th instar nymph/puparium. It has been demonstrated in *T. vaporariorum*, *B. tabaci* and other species that their morphology confusingly varies according to the structure, especially the hairiness, of the host leaf.

The ALEYRODINAE contain most species. ALEURODICINAE, differing in having large compound wax glands in the nymph/puparium in addition to simple ones, are represented in Australia by *Synaleurodicus hakeae* and *A. destructor*. [Dumbleton 1956; Mound and Halsey 1978; J. H. Martin 1985]

Superfamily APHIDOIDEA

by M. CARVER

Polymorphic and predominantly parthenogenetic, the most common morphs being apterous and alate parthenogenetic females. Fore wing venation comprising a composite longitudinal vein ending in a pterostigma, from which branch 3–4 oblique veins (RP, M, CuA₁, CuA₂); hind wings smaller, with 0–2 oblique veins. Eyes either compound with an appended ocular tubercle (triommatidion or 3-lensed eye) or, in some apterae, merely a triommatidion. Ocelli 3, present in alatae only. Antennae maximally 6-segmented, with, apically, a processus terminalis. Rostrum (labium) 4–5-segmented; 2nd segment telescopic into 1st. Tarsi 2-segmented, basal segment

small; empodium of 2 hairs. Apteræ usually soft bodied, with reduced body segmentation; some morphs coccidiform and with reduced morphology. Malpighian tubules absent. Predominantly feeders in phloem. With 4 nymphal instars.

The classification of Eastop (1977) is adopted. The Aphididae correspond to the Aphidoidea of Heie (1980).

The greatest development of the Aphidoidea is in temperate Holarctic regions. Of about 4700 described species world-wide (Eastop and Hille Ris Lambers 1976), 163 spp. in 84 genera are known from Australia. Only about 20 spp. are endemic and about as many again are common to the Asian fauna; the rest are exotic or cosmopolitan, some undoubtedly the result of accidental

introduction on cultivated plants by early British settlers.

Aphidoidea are believed to have originated on conifers in the Triassic or earlier and to have diversified rapidly in the late Cretaceous with the formation and predominance of the angiosperms. All extinct and extant aphidoid groups are represented in that time period. Plesiomorphy and apomorphy are not easily determinable, due to the reduced morphology of aphids, and the frequency of character changes, but their past and present host plant relationships provide valuable evolutionary clues. Probably, parthenogenicity appeared early and preceded viviparity. Adelgidae and Phylloxeridae are together the sister group of the Aphididae. The Aphidinae have only recently become the most species-rich group.

Key to the Families of Aphidoidea

1. Parthenogenetic ♀♀ viviparous (red-eyes of embryos usually visible through integument, or their curled stylets in macerated specimens); sexual ♀♀ oviparous. Antennae 4–6-segmented; usually, apical segment with well-delimited processus terminalis; 1 primary rhinarium basal to processus terminalis and 1 subapically on penultimate segment; other (secondary, adult) rhinaria present in most alatae and some apterae, usually concentrated on segment III. Eyes of apterae compound or 3-faceted. Siphunculi and cauda usually present. If apterae discoid and coccidiform, and antennae, triommatidia, labium, tarsi, siphunculi reduced or absent, then subanal plate bilobed. Fore wings: RP mostly present, M simple or 1- or 2-branched. Hind wings mostly with 2 oblique veins (Figs 30.4D, 18, 19A–C). Sexuales (with some exceptions) normal-sized, rostrate **Aphididae**
- All females oviparous. Antennae of (parthenogenetic) apterae very short, 3-segmented, with 1–2 rhinaria; of alatae 3–5-segmented, with 2–3 rhinaria; processus terminalis not or hardly delimited. Eyes of apterae 3-faceted. Siphunculi absent, cauda not evident. Subanal plate simple. Fore wings: RP absent, M simple. Hind wings with 0–1 oblique veins. Sexuales small, larviform, the sexual ♀ laying only 1 egg 2
- 2(1). Antennae of apterae 3-segmented, with 2 rhinaria; of alatae 5-segmented, with 3 rhinaria. Wings held roof-like in repose; CuA₁ and CuA₂ of fore wing separate; hind wing with 1 oblique vein. Ovipositor present (Fig. 30.19F). Sexuales rostrate. On conifers **Adelgidae**
- Antennae of apterae 3-segmented, with 1 rhinarium (Fig. 30.19D); antennae of alatae 3-, rarely 4-segmented with 2 rhinaria (Fig. 30.19E). Wings held flat over abdomen in repose; CuA₁ and CuA₂ of fore wing united basally; hind wing without oblique veins. Ovipositor absent (present in 1 extra-Australian species). Sexuales arostrate. On deciduous, dicotyledonous trees and vines **Phylloxeridae**

8. Aphididae (Figs 30.4D, 9B, 18, 19A–C). Wings tectiform or, less often, held flat in repose (e.g. Hormaphidinae). CuA₁ and CuA₂ usually separate, united basally in some Pemphiginae and Hormaphidinae. Paired siphunculi marginally on or near T5, varying from rings to long, cylindrical tubes; producing alarm pheromones. The modified apical segment, or cauda, variously shaped; serves to dispel excreted honeydew from body. Ovipositor absent. Sexuales alate (especially males) or apterous (females of most species), rarely larviform; larviform, arostrate and female uniparous in Pemphiginae. Monoecious or heteroecious.

Aphids are successful, largely because of their high fecundity. Parthenogenesis, viviparity and polymorphism, together, have made possible the telescoping of generations and consequently a high reproductive rate, and a division of labour with some morphs concentrating on reproduction and others on dispersal. The development of complex life cycles and specialised host plant relationships have also contributed. Exceptions and variations are common but, basically, in the life cycle of an aphid, sexuality and oviparity are restricted to only one generation annually, the final one in autumn, when sexual, oviparous

females (*oviparae*) and males are produced. The fertilised egg is the overwintering stage. The generation (of *fundatrices*) hatching from the eggs and all subsequent generations (*viviparae*) until the final one consist of parthenogenetic, viviparous females. Viviparae may be apterous or alate; the latter disperse to other hosts within the host range.

Heteroecy, or alternation of hosts, is practised by a small proportion of Aphididae, and involves migration of a species from its usually deciduous, woody (primary) host, following leaf ageing in early summer, to taxonomically unrelated herbaceous (secondary) host(s) and, following their deterioration in autumn, a return to the woody host for overwintering purposes. *Cavariella aegopodii*, the carrot-willow aphid (Aphidinae), is a typical heteroecious species. The fundatrix hatching in spring on the primary host, *Salix* (willow), is the foundress of generations of viviparae, which in the later generations are predominantly or exclusively alate; these abandon willow and fly to the secondary hosts, in this case, umbellifers such as carrot, parsley or fennel, on which several viviparous generations may be passed. Then, in autumn, migrant alate viviparae (*gynoparae*) and alate males are

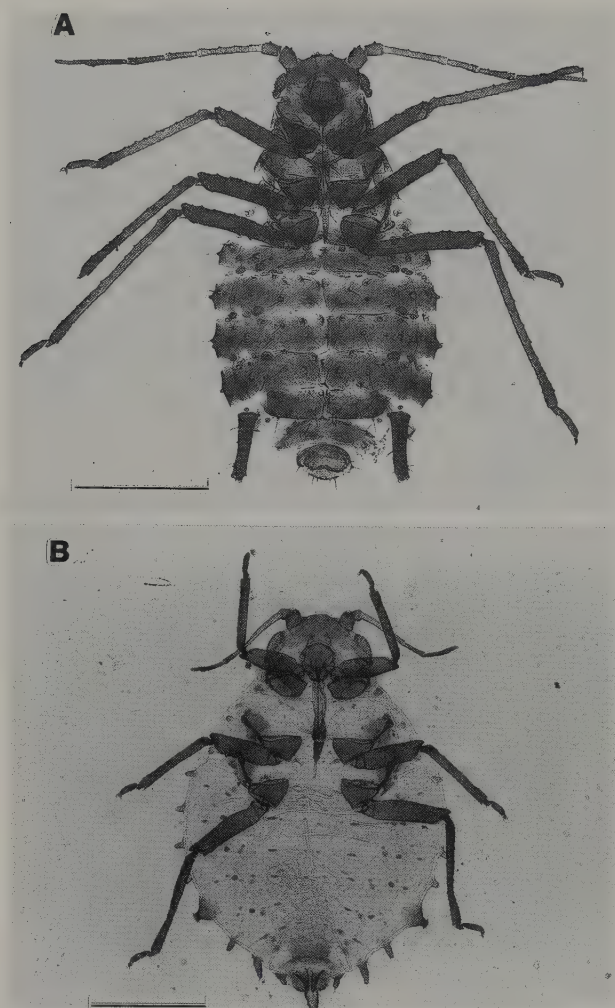


Fig. 30.18 Aphididae: A, aptera vivipara of *Meringosiphon paradiscum*; B, same of *Taiwanaphis tasmaniae*. Scale = 0.5 mm.

[J. P. Green, M. Carver]

produced; these fly to the primary host, on which the gynoparae reproduce the oviparae. Males and oviparae mate; fertilised, overwintering eggs are laid, and the cycle is complete. In (monoecious and) heteroecious Pemphiginae, Hormaphidinae and Anoeciinae, males are apterous and are produced on the primary host, often from the same mother (a *sexupara*) as the oviparae.

Complete cycles (holocycles), involving eggs in winter diapause, are obligatory in cold climates, and for species monoecious on deciduous trees. Australian examples of the latter are the exotic *Calaphis* and *Euceraphis* on birch, *Drepanosiphum* (Drepanosiphinae) on sycamore and *Periphyllus* (Chaitophorinae) on maple. In more temperate regions, where the autumnal environment is not extreme enough to induce the production of sexuales, and where suitable host plant material may remain available throughout the year, continuous parthenogenetic reproduction is possible. Such anholocyclic reproduction is prevalent among the exotic species in Australia, e.g. *Aphis spiraeicola*, *Aulacorthum solani*, *Brachycaudus helichrysi*, *Hyalopterus pruni*, *Macrosiphum euphorbiae*, *M. rosae*, *Metopolophium dirhodum* (Aphidinae), *Cinara*

spp. (Lachninae). Holocyclic and anholocyclic reproduction commonly co-exist in both monoecious and heteroecious species. Examples of the latter in Australia are the exotic *Myzus persicae* (Fig. 30.20), *Cavariella aegopodii*, *Capitophorus elaeagni*, *Hyperomyzus lactucae* (Aphidinae) and *Pemphigus bursarius* (Pemphiginae). Species such as *Rhopalosiphum padi* cannot be holocyclic, even though males are common, because the primary host is absent. In some species, sexuales are unknown (world-wide), e.g. *Aphis nerii*, *Toxoptera* spp., *Brachycaudus persicae*, *Myzus ornatus*, *M. ascalonicus*.

In Australia, the long, hot dry summer is a limiting factor for aphids and, in general, aphids are plentiful only in spring and autumn (Hughes *et al.* 1965). The indigenous species *Neophyllaphis brimblecombei* and *N. gingerensis* on *Podocarpus* and *Taiwanaphis furcifera* (Drepanosiphinae) on *Nothofagus* have overcome summer conditions by having a prolonged egg stage; sexuales are produced in spring and early summer concurrently with the viviparae and the resultant eggs do not hatch until the following spring (Carver and Hales 1974; Hales 1976). In Australia, sexuales and eggs of the Australasian *Schoutedenia ralumensis* (Greenideinae) on *Breynia* are produced concurrently with viviparae throughout summer and autumn (Hales and Carver 1976).

The various morphs differ both morphologically and physiologically, to a greater or lesser extent. A noteworthy morph is the *aestivalis* of *Periphyllus* (Chaitophorinae), a flattened, waxy, foliate or hirsute, 1st instar nymph, specialised for oversummering. Those of *P. californiensis* are common in Australia on Japanese maple. The most unusual aphid morph is the soldier, which is the specialised 1st or 2nd instar nymph of some Hormaphidinae and Pemphiginae, and represents the only known instance of altruistic social behaviour in Hemiptera. Depending on species, some or all of the 1st instars of a colony may become soldiers which, together, will attack and kill an intruding predator, using pointed frontal horns or the feeding stylets as piercing weapons, and greatly enlarged, raptorial fore, or fore and mid, legs for gripping. The soldier may either not moult and reproduce, or may moult to a normal, non-aggressive instar (Aoki 1982). In Australia, *Pseudoregma panicola* and *Ceratovacuna* sp. (Hormaphidinae) produce soldiers.

The factors influencing polymorphism are complex and interacting. Briefly, the production of sexuales is induced by low temperatures and short photoperiod, in combination; and by reduction in host plant quality. Alatae are formed in response either to increased body contact resulting from crowding or to reduced host plant quality. Ant attendance and parasitism suppress alatifformity. Intrinsic timing mechanisms of unknown nature are also believed to operate.

The fundatrices, being the product of sexual union, each have a different genotype, but each fundatrix and its descendants are genotypically identical. Thus populations tend to be clonal. The parthenogenetic female is diploid (XX) and there is no reduction division. So are her male progeny, but they are XO, one X-chromosome being lost during the single maturation division of a presumptive

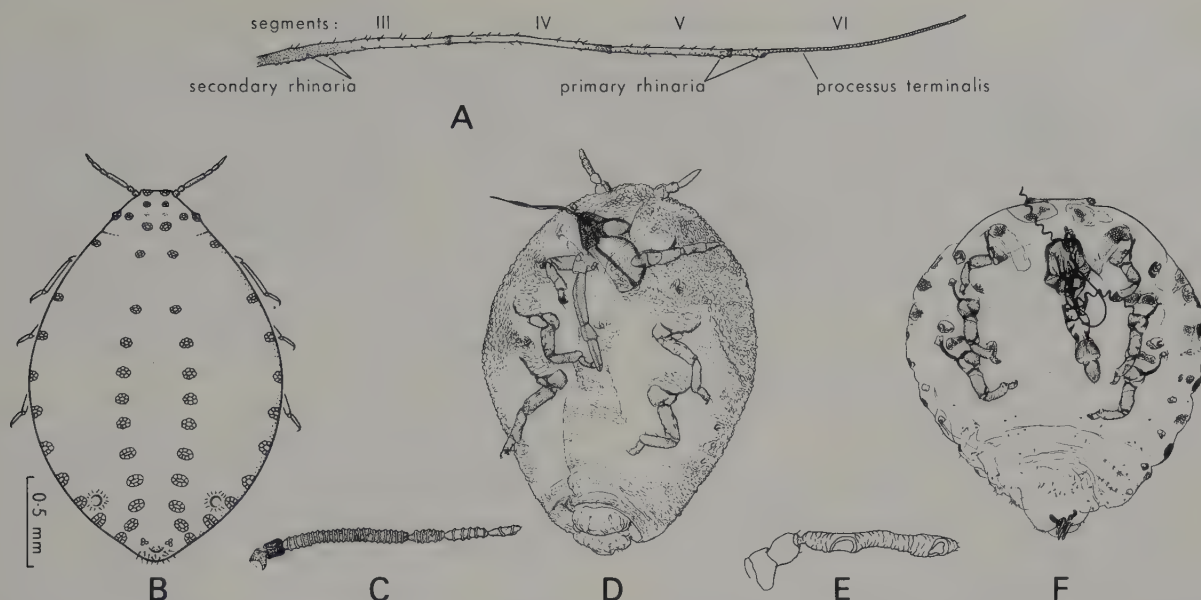


Fig. 30.19 A, *Macrosiphum rosae*, Aphididae, antenna of aptera vivipara; B, *Eriosoma lanigerum*, Aphididae, aptera vivipara, dorsal aspect; C, antenna of alata vivipara; D, *Daktulosphaira vitifoliae*, Phylloxeridae, apterous parthenogenetic ♀, ventral aspect; E, antenna of alata; F, *Pineus pini*, Adelgidae, apterous parthenogenetic ♀, ventral aspect. [A, C–F after Eastop 1966; B by S. P. Kim]

male oocyte. All functional sperm carry one X, spermatocytes without an X-chromosome degenerating. Thus all fertilised eggs are female (XX).

Some Pemphiginae, Hormaphidinae, Tamaliinae and Aphidinae, especially heteroecious species, induce gall formation on the primary host. Few species induce galls in Australia; most familiar are the purse-shaped galls of *Pemphigus bursarius* on petioles of poplar, the nodosities on twigs and roots of apple caused by *Eriosoma lanigerum*, and leaf curl of peach by *Myzus persicae*.

The few other Australian Pemphiginae live anholocyclically underground, mostly on grass roots. Of the Aphidinae, *Rhopalosiphum rufiabdominalis* and *R. insertum* are anholocyclic on grass roots and *Brachycaudus persicae* on roots of peach, the latter ascending to the leaves when these become favourable.

Exotic aphids are rare on the native flora. *Cinara* spp. are found on conifers; *Brevicoryne brassicae* and *Lipaphis erysimi* infest crucifers; *Aphis craccivora* is found mainly on Fabaceae; *Therioaphis trifolii* f. *maculata* (spotted alfalfa aphid), *Acyrtosiphon kondoi* (blue-green aphid) and *A. pisum* on lucerne and other Fabaceae; *Toxoptera citricidus* on citrus; *Macrosiphum rosae* on rose; *Neotoxoptera formosana* on *Allium*; *Rhopalosiphum padi*, *R. maidis*, *Sitobion* spp. and *Metopolophium dirhodum* on grasses and cereals. *Macrosiphum euphorbiae*, *Myzus persicae*, *M. cymbalariae*, *Neotoxoptera oliveri*, *Aulacorthum solani* and *Aphis spiraecola* are polyphagous to differing degrees, with *A. spiraecola* preferentially infesting woody Rosaceae and herbaceous Asteraceae. *Rhopalosiphum nymphaeae* colonises (the upper surfaces) of diverse aquatic plants. However, the wide host ranges of several of the economically important and other common species may obscure the fact that most aphids are highly host-specific.

Aphids are pests both directly as sap-feeders and pollutive excreters, and indirectly as vectors of plant virus diseases. *Myzus persicae* is the most vectorial, transmitting, among many others, potato leaf roll and beet western yellows viruses. The other important virus vectors in Australia are *Rhopalosiphum padi* and *Metopolophium dirhodum* (barley yellow dwarf virus of cereals), *Hyperomyzus lactucae* (lettuce necrotic yellows virus) and *Pentalonia nigronervosa* (banana bunchytop virus).

Imported aphidiine parasites (HYMN: Braconidae)

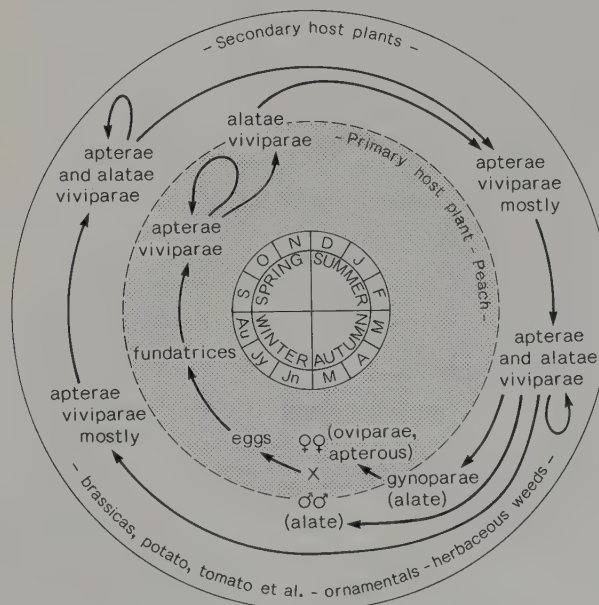


Fig. 30.20 Phenology of *Myzus persicae*, Aphididae, in Australia.

[S. Smith]

have been used successfully to help control *Therioaphis trifolii* f. *maculata*, *Acyrtosiphon kondoi*, *Hyperomyzus lactucae* and other species (Carver 1989). *Eriosoma lanigerum* is considered to be under successful biological control by *Aphelinus mali* (HYMN: Aphelinidae). *Aphis chloris* has become established as a biological control agent of *Hypericum perforatum* (St John's wort).

Aphid-ant mutualism is similar in Australia to elsewhere. The same aphid species are involved and to a similar degree. *Anomalaphis comperei* and *Aphis acae-novinae* are the only indigenous aphids known to be ant-attended.

The indigenous species, representing three subfamilies, are restricted to native plants and are for the most part phylogenetically isolated.

Of the DREPANOSIPHINAE, *Neophyllaphis* (11 spp.) is mainly associated with the ancient conifer *Podocarpus* and is of circumantarctic distribution with species extending to Africa and Japan. Three Australian species colonise *Podocarpus* and one occurs on *Araucaria*. *Neophyllaphis* has many ancestral and unique features including alate or alatoid oviparae, each possessing a large, setaceous, bipartite subgenital plate, and a large, globular, glandular, wax-covered cauda. Eggs of the Australian spp. on *Podocarpus* are exceedingly flat and membrane-covered, a feature shared only by *Taiwanaphis*. All morphs and instars of some species possess large, eversible, segmental, adhesive vesicles on the abdominal venter, structures which are peculiar to *Neophyllaphis* and two South American *Paoliella* (Carver 1971; D. White and Carver 1971; Hales 1976). *Ceriferella* (2 spp.) colonises *Leucopogon* (Epacridaceae, also Gondwanan, and the Australian counterpart of Ericaceae). The wax-covered body of the aptera resembles the white, bearded flowers of its host. A mosaic of unusual features includes characteristic wax gland plates and a proximally curving oblique vein in the hind wing (Carver and Martyn 1965). *Taiwanaphis* (= *Sensoriaphis*) is closely related to *Neuquenaphis* on *Nothofagus* in South America. Five spp. of *Taiwanaphis* are known from *Nothofagus* (Fagaceae) in eastern Australia, New Zealand and New Guinea; 1 sp. from *Melaleuca* (Myrtaceae) in W.A., where *Nothofagus* is extinct; and 9 spp. from other Myrtaceae in Asia. The distribution is a rare example of successful host transference consequent upon loss (extinction) of the original host (Carver 1978). The ovipara may possess, like *Neuquenaphis*, two pairs of unusual, large, ventral, abdominal wax plates, producing wax flakes to cover the flat eggs, and may have, like South American *Lizerius*, scent plaques on all tibiae (Carver and Martyn 1962; Carver and Hales 1974). The abbreviated life cycles of some of the above species have already been noted.

The GREENIDEINAE are a predominantly Asian group, most species having in common setiferous siphunculi and circumanal wax glands. *Anomalaphis* (6 spp.) on *Agonis*, *Leptospermum* and *Astartea* (Myrtaceae) and *Meringosiphon* (1 sp.) on *Oxylobium* (Fabaceae) are Australian with several related genera in the Orient, South Africa and South America. The ovipara of *Anomalaphis*

comperei also has scent plaques on all tibiae (Carver 1959, 1971). *Schoutedenia ralumensis*, widespread throughout Asia on woody Euphorbiaceae, occurs in eastern Australia on *Breynia* and *Phyllanthus* and the ovipara, like *Eonaphis* of South Africa, bears scent plaques on the hind femora, not the tibiae (Hales and Carver 1976).

The few indigenous APHIDINAE include *Aphis acae-novinae* on *Acaena* (Rosaceae) and *A. platylobii* on *Platylobium* and *Daviesia* (Fabaceae), noteworthy for relatively long siphunculi (Eastop 1961; Carver and White 1970). [Cottier 1953; Eastop 1966; Blackman 1974; Heie 1980; Blackman and Eastop 1984; Dixon 1985; Minks and Harrewijn 1987–89]

9. Adelgidae (Fig. 30.19F). Hind wings with 1 oblique vein. Wax glands abundant in all morphs. Ovipositor present. Sexuales small, larviform, rostrate, with 4-segmented antennae; sexual female uniparous. All females, both parthenogenetic and sexual, are oviparous.

Overwintering of fundatrix as 1st (rarely 2nd) instar nymph is unique. Heteroecious. Hosts are conifers (Pinaceae); primary host, *Picea* (spruce); secondary hosts, *Abies*, *Larix*, *Pseudotsuga*, *Tsuga* and *Pinus*. Highly host-specific. True galls formed on primary host. Complete life cycle complex, typically involving several morphs and only 5 generations on 2 hosts over a period of 2 years. First instar fundatrices overwinter on *Picea*. The 2nd generation (*gallicolae*), as immatures, induce formation of cone-like galls and, as alate adults, migrate to secondary hosts, where their progeny (3rd generation) overwinter as 1st instars. Some of 4th generation are alate sexuparae, which fly to *Picea* and produce the sexuales. Fundatrices hatch promptly from the resultant fertilised eggs, and the cycle is complete. Instances are becoming increasingly known of variously incomplete but always agamic cycles.

Holarctic. Only 8 genera and about 50 spp. world-wide. Only 3 spp., all exotic, are definitely known from Australia: *Adelges* sp. or spp. on *Picea* and *Pseudotsuga* (Douglas fir), and *Pineus* sp. or spp. on *Pinus*. The anholocyclic species widespread on *Pinus radiata* is probably *Pineus pini*. [Heinze 1962; Shaposhnikov 1967; C. I. Carter 1971]

10. Phylloxeridae (Figs 30.19D, E). Hind wings without oblique veins. Faceted wax glands in 1 genus only. Anus absent. Ovipositor (small) in 1 species only. Parthenogenetic and sexual females oviparous.

Fundatrix overwinters in egg stage. Hosts are deciduous trees and vines mainly in families Juglandaceae, Fagaceae and Vitaceae. Blister-like galls on foliage in some genera. Phylloxeridae are predominantly monoe-cious. However, a few *Phylloxera* in Europe alternate between species of *Quercus* (Fagaceae)—rare instances of intrageneric heteroecy—and, in North America, between *Carya* (Juglandaceae) and *Quercus* or *Castanea* (Fagaceae) (Börner and Heinze 1957; Stoetzel 1985).

Holarctic, with about 70 spp. world-wide.

Daktulosphaira [= *Viteus*] *vitifolii* is the notorious grape phylloxera, a native of eastern and southern U.S.A.; this aphid devastated the vine crops of Europe in the 1870s and 1880s after its accidental introduction there on imported American vines. On its natural hosts, e.g. *Vitis*

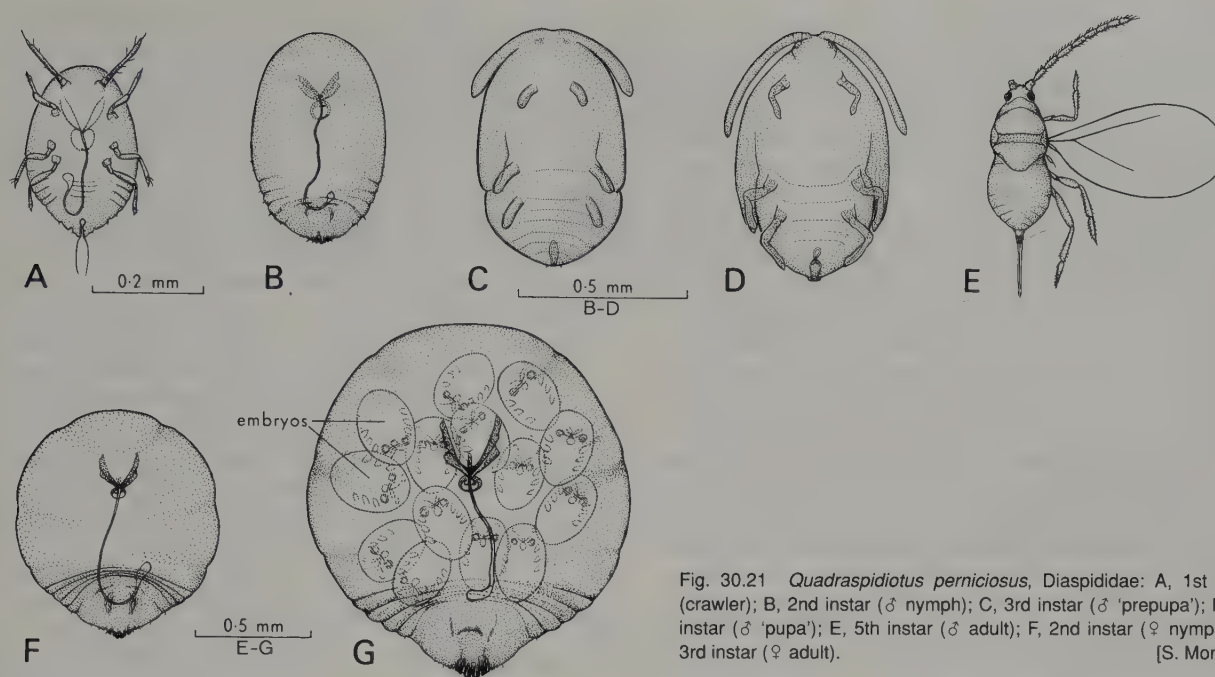


Fig. 30.21 *Quadraspidiotus perniciosus*, Diaspididae: A, 1st instar (crawler); B, 2nd instar (♂ nymph); C, 3rd instar (♂ 'prepupa'); D, 4th instar (♂ 'pupa'); E, 5th instar (♂ adult); F, 2nd instar (♀ nymph); G, 3rd instar (♀ adult). [S. Monteith]

riparia and *V. rupestris*, *D. vitifolii* is normally heteroeccious between the leaves and roots. The fundatrix forms blister-like galls on the underside of leaves; its descendants are also gallicolous (gallicolae), or migrate to the roots (*radicicolae*) in increasing numbers as the leaves age, where they induce the formation of nodose and tuberose galls on the roots. Subsequent generations of *radicicolae* may hibernate as 1st instar nymphs, or produce alate sexuparae, the only alate morph in the cycle. The sexuparae emerge from the soil and produce the small, arostrate sexual females and males on nearby aerial parts of the vine. The resultant fertilised eggs overwinter. *D. vitifolii* is normally not injurious to these hosts.

On the European vine, *V. vinifera*, *D. vitifolii* is not holocyclic. This host is not acceptable to the highly host-specific fundatrix, but its roots are highly susceptible to the *radicicolae*, and continuous, anholocyclic reproduction may occur on the roots, often with damaging consequences.

Damage by phylloxera has been successfully controlled by the widespread use of phylloxera-resistant/tolerant rootstocks of American *Vitis*. *D. vitifolii* is present in Vic. and N.S.W., where it can be holocyclic when American rootstocks put up aerial suckers, but it has not been a serious problem for many years (Galet 1982; Buchanan and Hardie 1978).

Only two other phylloxerids are known from Australia, *Phylloxera salicis*, a glanduliferous species on bark of *Salix*, and the tuberculate *Moritzziella corticalis* on *Quercus*, also on bark. [Heinze 1962; Shaposhnikov 1967]

Superfamily COCCOIDEA

by D. J. WILLIAMS

This group, commonly known as scale insects and mealybugs, contains more than 6000 described species and

as many again remain undescribed (D. R. Miller and Kosztarab 1979). The Australian fauna, of about 840 known species, is one of the most interesting.

Coccoidea are highly sexually dimorphic. The adult female (Figs 30.22–25) is sedentary, larviform and apterous, with the head and thorax fused, and abdominal segmentation often ill defined. Legs are often reduced, or absent, the insect being anchored to the host plant principally by its stylets. Diverse adaptations protect the female and its progeny from desiccation and predation. The integument may be greatly thickened, that of the eriococcid *Epicoccus* being an extreme example (Lower 1957), or scale-like or wax producing, or a separate scale may be secreted (Diaspididae). Gall initiation is remarkably developed in some Australian Eriococcidae. Eggs may be protected under the body, in special ovisacs produced at the end of the body or, as in some Margarodidae, in a special internal sac ('marsupium'). Waxy secretions also provide protection from contamination by excreted honeydew. The latter may be forcibly ejected some distance from the insect, or may be removed by ants.

The adult male (Fig. 30.25A), in contrast, lacks functional mouth-parts and is usually fragile and short lived. The male is alate or, less often, apterous; intermediates also occur. Some species exhibit alary dimorphism. The alate male is always only two-winged, the hind wings being reduced to *hamulohalteres*.

Whereas the female functions to promote high fecundity and the male to promote outbreeding, the main agent for dispersal is the 1st instar or crawler, which is highly mobile, with well-developed legs and antennae and, being small and light in weight, is easily dispersed by wind. First instar females of *Cystococcus* (Eriococcidae) are phoretic and disperse by attaching themselves to the abdomen of adult male brothers (Gullan and Cockburn 1986). Subsequent nymphal instars of most Coccoidea

become predominantly or permanently sedentary, with the legs reduced or absent. Both male and female nymphs of scale-producing species secrete a scale covering. Females have 2 or 3 pre-imaginal instars and males always 4. The penultimate and final nymphal instars of males are stationary, non-feeding (alabiate), metamorphic phases, and are termed pupal instars.

Reproduction is oviparous, ovoviviparous or viviparous. Some species are parthenogenetic. Seven different types of parthenogenesis have been recognised (Nur 1971, 1980; Brown and Chandra 1977), making the Coccoidea, cytologically, highly complex. *Icerya purchasi* and some other *Icerya* spp. (Margarodidae) are hermaphroditic.

Species of *Kerria* (Kerriidae) are a source of lac. The red dyes cochineal and kermes are produced from species of *Dactylopius* (Dactylopiidae) and *Kermes* (Kermesidae). Many Coccoidea are important pests of perennials, affecting crops in agriculture, horticulture and forestry.

Some of Australia's worst coccoid pests have been accidentally introduced; they frequently escape detection at quarantine inspection because of their sessile and often cryptic habit. Conversely, catastrophic outbreaks occurred in other parts of the world following the introduction of the Australian species *Icerya purchasi* (Margarodidae) and *Pseudococcus calceolariae* (Pseudococcidae), which were subsequently controlled by natural enemies exported from Australia (F. Wilson 1963). Other coccoids are useful in the biological control of weeds (F. Wilson 1960).

Banks (1977) studied the pigments and the chemotaxonomic relationships of some Australian Coccoidea.

There is no general acceptance of a system of classification. One system is based on the structure of the labium (Koteja 1974a, b). For purposes of identification, a classification based on adult female morphology is most practical; but classifications should also take into account features of adult males, immatures, cytology and biology. [Beardsley and González 1975; Koteja 1985]

Key to the Families of Coccoidea Known in Australia—Adult Females

1. Abdomen with 2–8 pairs of spiracles; thoracic spiracles also present (Figs 30.23A, C)..... 2
Abdominal spiracles absent 3
- 2(1). Anal opening dorsal, surrounded by 6 setae and a band of pores; antennae with 3–8 segments, terminal segment with a stout apical spur (Figs 30.23A, B) **Ortheziidae**
Anal opening apical to dorsal in position, simple, sometimes not discernible, never immediately encircled by pores and setae although anal tube present with its inner end often surrounded by a band of pores; antennae with 6–11 segments in Australian species, reduced to tubercles in some extra-Australian species, terminal antennal segment without apical spur (Figs 30.22C, 23C) **Margarodidae**
- 3(1). Anterior thoracic spiracles much larger than posterior pair; brachial plates (Fig. 30.23F) present on thorax; abdomen with large dorsal spine near centre; posterior end of abdomen attenuated into an anal tubercle bearing an anal ring comprising 10 setae and an anal fringe surrounded by a ring of points and fimbriations **Kerriidae**
Thoracic spiracles approximately the same size; brachial plates and dorsal spine absent; anal opening varying in position, either external or at base of small anal tube, with or without setae and pores, but never with an anal tubercle bearing an anal fringe, points and fimbriations 4
- 4(3). With a pair of triangular or rounded plates at base of anal cleft (Fig. 30.24A), the mesal margins of plates contiguous **Coccidae**
Without a pair of such plates at base of anal cleft, although there may be a small single plate in this position (Fig. 30.24B) 5
- 5(4). 8-shaped pores present (Figs 30.24C, D), sometimes few 6
8-shaped pores absent entirely 8
- 6(5). Anal plate, if present, poorly developed; cribriform (sieve-like) plates absent; tubular ducts present, inner end slightly angled, but without filament (Fig. 30.24D) **Asterolecaniidae**
Anal plate well developed dorsally, either entire or deeply bilobed; cribriform plates present (Fig. 30.24C), at least on dorsum of abdomen; tubular ducts each with large and sometimes slender filament on inner end 7
- 7(6). Antennae 1-segmented, with a group of quinquelocular (5-locular) pores near base; anal plate triangular or shield-like; arched plate above anal ring absent; venter with rows of 8-shaped pores on abdomen (Fig. 30.24B) **Cerococcidae**
Antennae 7–9-segmented, without quinquelocular pores near base; anal plate bilobed, often 'butterfly-shaped', a small arched plate situated above anal ring, occasionally joined laterally with anal plate; venter without transverse rows of 8-shaped pores (Fig. 30.24C) **Lecanodiaspididae**
- 8(5). Clusters of 3-, 4- or 5-locular pores scattered over dorsum, each cluster with a common duct; thick, approximately parallel-sided, truncate setae present (Fig. 30.23I) **Dactylopiidae**
Clusters of 3-, 4- or 5-locular pores absent on dorsum, if clusters of pores present then the pores are multilocular; setae usually acute but may be apically truncate 9
- 9(8). Terminal segments of abdomen fused into a pygidium or pygidium-like area (Figs 30.24E–G) 10
Terminal segments of abdomen not fused into a pygidium 12
- 10(9). Antennae segmented; legs usually present; multilocular disc pores present, often 'flower-shaped' or star-shaped; quinquelocular pores absent; scale covering not incorporating exuviae of previous instars (Fig. 30.24E) **Conchaspidae**
Antennae each reduced to a tubercle; legs always absent; multilocular disc pores absent; disc pores, if present, quinquelocular or trilocular; scale covering, if present, incorporating exuviae of previous instars 11

- 11(10). Pygidium of adult ♀ with ducts and a marginal fringe of plates or gland spines and lobes (Fig. 30.24G); scale incorporating exuviae of 1st and 2nd instars; adult ♀ sometimes remaining enclosed within exuviae of 2nd instar; without operculum **Diaspididae**
- Pygidium of adult ♀ simple, without lobes, plates or gland spines; adult ♀ always enclosed within 2nd instar exuviae; dorsum of posterior end of 2nd instar forming a flat anal plate or operculum, surrounded by a sclerotised rim (Fig. 30.24F) **Halimococcidae**
- 12(9). With a combination of dorsal ostioles, ventral circuli, trilocular pores and usually 1–18 pairs of cerarii (Fig. 30.23G); anal ring often with an outer and an inner row of pores; tubular ducts not cupped at inner end **Pseudococcidae**
- Without dorsal ostioles, ventral circuli and cerarii (Figs 30.23E, H); anal ring usually with a single row of pores; tubular ducts, if present, with inner end invaginated, forming a cup **Eriococcidae**

11. Margarodidae (Figs 30.22, 23C, D, 25A). This family is regarded as the most primitive of the Coccoidea. Some males with compound eyes; adult female often without functional mouth-parts, usually with abdominal spiracles; anal opening simple, usually with internal anal tube, or tube absent.

At least 12 Australian genera are known. The family contains some of the largest coccoids; females of the Australian genus *Callipappus* may attain a length of 40 mm (Froggatt 1921b; Morrison 1928). *Icerya purchasi*, the cottony cushion or fluted scale, is native to Australia where *Acacia* is its natural host. Towards the end of last century it was accidentally introduced to California where it devastated the citrus industry. The Australian coccinellid *Rodolia cardinalis* was exported for its control, giving rapid success (Koebele 1890; Riley 1890). Most Australian Margarodidae are endemic. *Auloicerya*, closely related to *Icerya*, feeds on *Acacia* or *Hakea*, while *Monophlebulus* and *Nodulicoccus* are primarily associated with *Eucalyptus* (Morrison 1928). *Conifericoccus agathidis*, the kauri coccid, has caused extensive defoliation of *Agathis robusta* in plantations in Qld (Brimblecombe and Heather 1965). *Eumargarodes laingi* and *Promargarodes australis* are probably introduced species and damage sugar cane in Qld. Their adult

females have large fossorial fore legs. The nymphs encyst in the soil and form 'ground pearls', which often are found in enormous numbers and remain quiescent during long periods of drought. [D. R. Miller 1984]

12. Ortheziidae (Figs 30.23A, B). This family is regarded as primitive because, like the Margarodidae, the female possesses abdominal spiracles and the adult male has compound eyes. However, the presence in the female of a setiferous and poriferous anal ring places the family in the lineage that includes all the remaining families (D. R. Miller 1984). The adult female secretes symmetrical wax plates on the dorsum, and a distinctive wax ovisac at the posterior end of the abdomen.

The family may have originated in the Cretaceous Africa-South America land mass and subsequently dispersed to other areas on Recent plant families (D. J. Williams 1984). About 80 species are known world-wide in six genera, *Orthezia* being the largest genus (Morrison 1925, 1952), but endemic species are absent in Australia. The introduced species are *Newsteadia floccosa*, which inhabits damp, cooler areas at soil level; *Nipponorthezia guadalcanalia*, known from Qld in litter; and *Orthezia insignis*, a polyphagous tropicopolitan species which can be troublesome in greenhouses.

13. Pseudococcidae (Figs 30.23G, 25F). These are the



Fig. 30.22 *Promargarodes australis*, Margarodidae. A, 1st instar; B, 2nd instar ♀ (cyst form); C, adult ♀.

[P. J. Gullan]

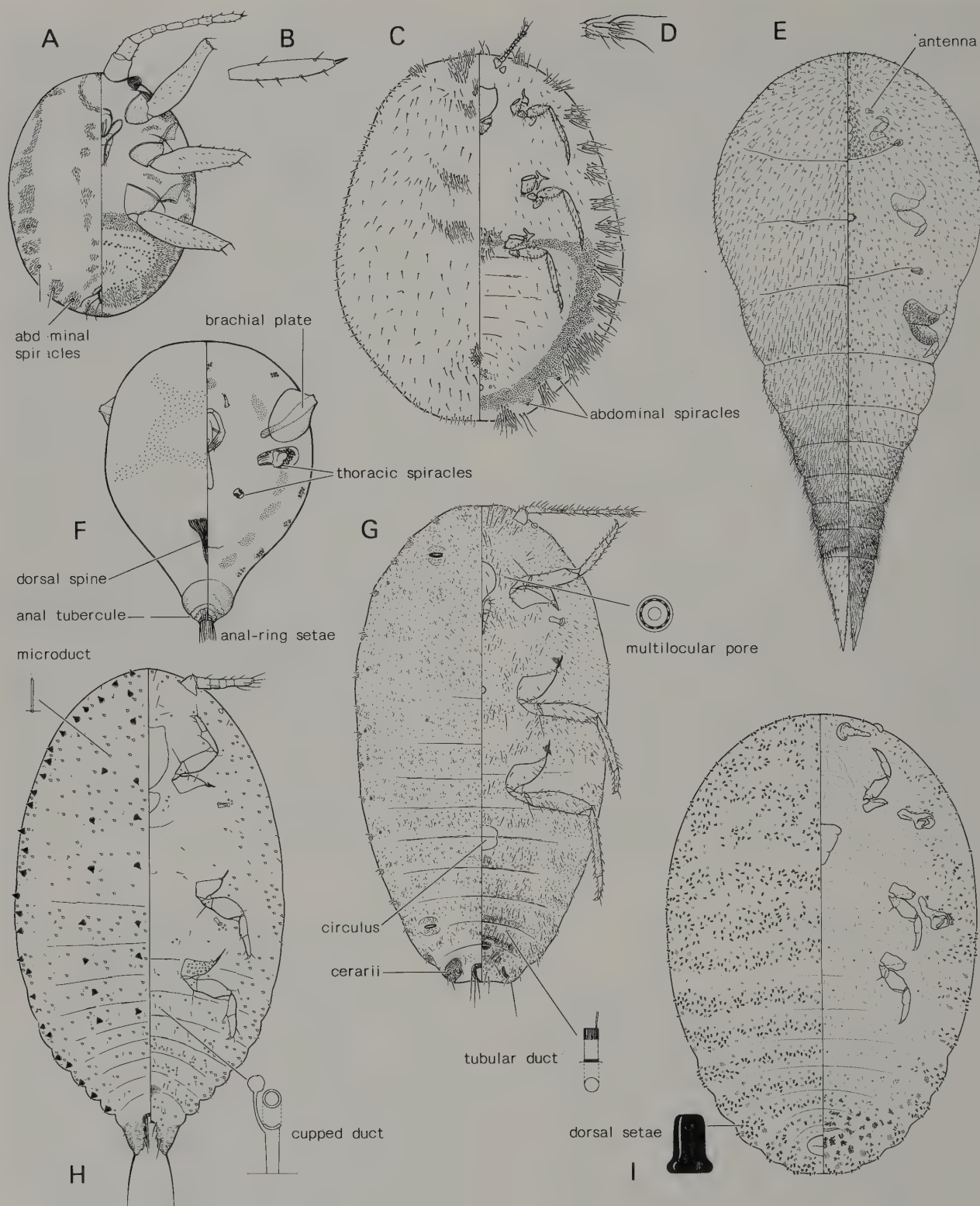


Fig. 30.23 Coccoidea, ♀♀ (macerated, slide-mounted specimens): A, *Orthezia insignis*, Ortheziidae, whole insect (after Morrison 1925); B, same, terminal antennal segment; C, *Icerya purchasi*, Margarodidae, whole insect (after Howell and Beshear 1981); D, same, terminal antennal segment; E, *Apiomorpha frenchi*, Eriococcidae, whole insect (after Gullan 1984a); F, *Austrotachardia angulata*, Kerriidae, whole insect (after Chamberlin 1923); G, *Pseudococcus calceolariae*, Pseudococcidae, whole insect (after D. J. Williams 1985); H, *Eriococcus ironsidei*, Eriococcidae, whole insect (after D. J. Williams 1973); I, *Dactylopius opuntiae*, Dactylopiidae, whole insect (after De Lotto 1974).

[S. Smith]

true mealybugs, so called because many species secrete a thin covering of mealy wax over the body surface. The family can be recognised by the presence of some or all of the following characters in the female: dorsal ostioles, ventral circulus, marginal cerarii, tubular ducts with the inner end either flat or rounded but never cupped, and the presence of trilocular pores at least on the dorsal surface.

The family is numerically one of the largest of the Coccoidea and contains many injurious species world-wide. Many of the endemic species cause little damage, but *Melanococcus albizziae* can kill *Acacia* and *Australicoccus grevilleae* is destructive to ornamental *Grevillea*. The cosmopolitan *Pseudococcus longispinus* which probably originated in Australia on native Rutaceae (Flanders 1940), is injurious to citrus in parts of Australia (Furness 1976, 1977). The polyphagous *P. affinis* is possibly introduced and is found on all parts of the plant; it is considered to be the most important of the underground mealybug pests of Australia. *Planococcus minor* (recorded as *P. citri*) is injurious to passion fruit in Qld (D. A. H. Murray 1978). *Hypogeococcus festerianus* has been successfully introduced from South America to control *Harrisia cactus* (*Eriocereus martinii*) in Qld (McFadyen 1986). [D. J. Williams 1985; D. J. Williams and Watson 1988]

14. Eriococcidae (Figs 3.14; 30.23E, H, 25B–E). More than 480 species are known world-wide (Hoy 1963). The family is probably paraphyletic (Cox and Williams 1986). Major characters of *Eriococcus* and related genera are well-developed anal lobes, a poriferous and setiferous anal ring, conical or bulbous dorsal setae, enlarged macroducts cupped at the inner end, microducts, quinquelocular disc pores, and small cruciform pores.

Australian species include some of the most bizarre of all the Coccoidea, many forming spectacular galls on endemic trees. *Apiomorpha* (39 spp.) is confined to *Eucalyptus*, on which it forms distinctive galls; galls of females occur on stems or leaves, those of males, usually much smaller, occur on stems, leaves and fruits or as outgrowths of the maternal gall (Gullan 1984a). *Cylindrococcus* forms conical to fusiform galls on *Allocasuarina* (Gullan 1984b), and *Sphaerococcopsis* blister-like galls on *Eucalyptus* (Beardsley 1974). Beardsley (1984) has discussed some other Australian gall-forming genera such as *Ascelis*, *Casuarinaloma* and *Floracoccus*.

Eriococcus coriaceus is a common pest of *Eucalyptus* in Australia and New Zealand (Patel 1971). Several species of *Eriococcus* are associated with *Leptospermum* (Hoy 1959); *E. orariensis* has been used successfully in New Zealand in the control of *L. scoparium*, a pest shrub of Australian origin. *E. ironsidei*, the macadamia felted coccid, is an important pest of macadamia in south-eastern Qld (Ironsides 1978). [Ferris 1955; Hoy 1962; D. J. Williams 1973]

15. Dactylopiidae (cochineal insects; Fig. 30.23i). The family is related to the Eriococcidae; both families possess tubular ducts cupped at the inner end (Fig. 30.23H), but in Dactylopiidae the anal opening is a simple slit with a crescentic anterior rim. *Dactylopius*, the only genus, originated in the New World on *Opuntia* cactus.

Dactylopius contains the red pigment cochineal or carminic acid; carmine dye, the hydrated aluminium chelate of carminic acid is produced commercially in some parts of the world from *D. coccus*.

Of the 9 species of *Dactylopius* (De Lotto 1974) 5, all of exotic origin, are known from Australia. *Opuntia* plants were first brought to Australia in the 18th century to establish a cochineal industry (Mann 1969, 1970) but became a menace on grazing and farming land until controlled by the introduction of *Cactoblastis cactorum* (LEPI: Pyralidae) and several species of *Dactylopius*.

16. Asterolecaniidae (Fig. 30.24D). The family, which formerly included the Cerococcidae and Lecanodiaspididae, is ill defined. Diagnostic characters of female are 8-shaped pores, tubular ducts without a normal slender filament, but with inner, short basal part slightly bent, and absence or extreme reduction of legs. The largest genus is *Asterolecanium* (Russell 1941), the 18 Australian species of which form pit scales on diverse plants. The adult female is normally enclosed in a glassy test. *Frenchia* (3 spp.), which has an elongate abdomen, is at present included in the family; species cause unusual galls on *Banksia* and *Casuarina* (Lambdin and Kosztarab 1981).

17. Cerococcidae (Fig. 30.24B). The family contains about 60 species world-wide in 3 genera, and is tropicopolitan with extensions into temperate regions. Important diagnostic characters include prominent anal lobes with a dorsal triangular anal plate at base, dorsal and ventral 8-shaped pores, dorsal, cribriform plates, tubular ducts cupped and with terminal filament at inner end, quinquelocular pores near antennal bases and in spiracular furrows, and legs absent or reduced to stubs. The group was formerly included in the Asterolecaniidae. Some workers regard Asterolecaniidae and Lecanodiaspididae as its closest relatives, others emphasise affinities with the Eriococcidae (Koteja 1974b).

Cerococcus is the largest genus, with 5 species in Australia on endemic woody plants. Their external waxy coverings are mostly stellate and reddish brown. [Lambdin and Kosztarab 1977]

18. Lecanodiaspididae (Fig. 30.24C). This small family of almost 70 known species is tropicopolitan with extensions into temperate areas. Its origins are possibly Gondwanan (Howell and Kosztarab 1972; Williams 1984). Important characters of female are dorsal 8-shaped pores, dorsal cribriform plates, and deeply bilobed, often 'butterfly-shaped' anal plate, at base of a cleft. Arched plate present above anal ring, and sometimes fused laterally with anal plate. Dorsal ducts with cup and filament at inner end. Quinquelocular disc pores usually present in spiracular furrows. Legs reduced or absent. Although formerly associated with the Asterolecaniidae, the combination of characters suggests affinities with the Coccidae (Lambdin and Kosztarab 1973).

Lecanodiaspis, *Gallinococcus*, *Brookesiella* and *Cela-tiococcus* occur in Australia, mainly on endemic trees and shrubs. Some are associated with Rutaceae, including citrus. [Lambdin and Kosztarab 1974; Lambdin *et al.* 1973; Howell *et al.* 1973]

19. Coccidae (Figs. 30.24A, 25G, H). This family com-

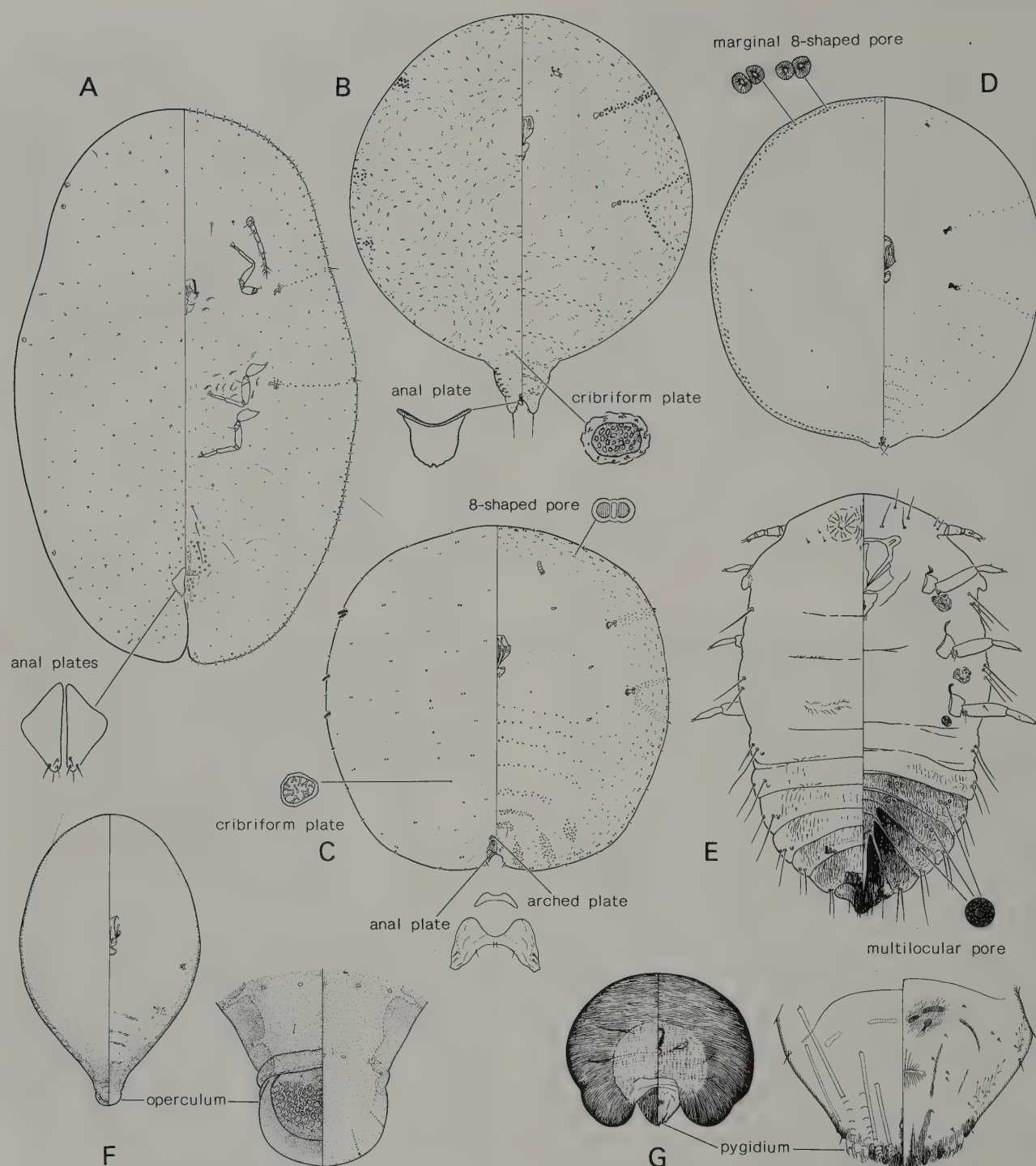


Fig. 30.24 Coccoidea, ♀♀ (macerated, slide-mounted specimens): A, *Coccus hesperidum*, Coccidae, whole insect (after Gill *et al.* 1977); B, *Cerococcus stellatus*, Cerococcidae, whole insect (after Lambdin and Kosztarab 1977); C, *Lecanodiaspis acaciae*, Lecanodiaspididae, whole insect (after Howell and Kosztarab 1972); D, *Asterolecanium hakeae*, Asterolecaniidae, whole insect (after Russell 1941); E, *Conchaspis angraeci*, Conchaspidae, whole insect (after Mamet 1954); F, *Colobopyga australiensis*, Halimococcidae, 2nd instar showing operculum (after Deitz 1979); G, *Aonidiella aurantii*, Diaspididae, whole insect showing pygidium (after McKenzie 1938). [S. Smith]

prises about 1000 species world-wide (Hamon and Williams 1984). Coccidae are usually easily recognisable by the presence in the female of paired triangular or rounded anal plates at the base of an anal cleft. Other important characters are spiracular and marginal setae and

tubular ducts with the inner end cupped. Many species produce wax in various forms, but others are naked. The dorsum of some is greatly convex. Coccidae and Eriococcidae may have common ancestry (D. R. Miller and González 1975).

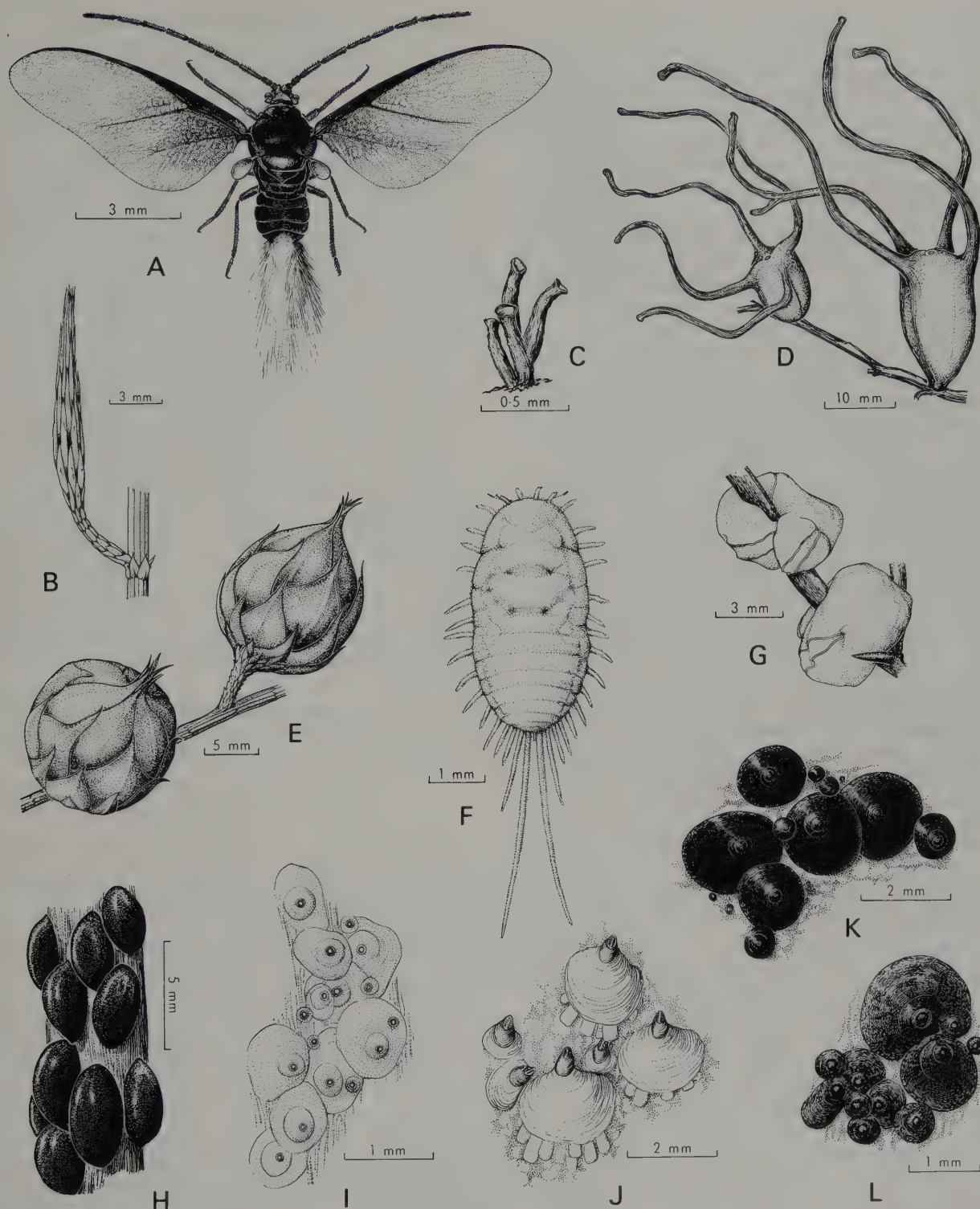


Fig. 30.25 Coccoidea: A, ♂ of *Callipappus* sp., Margarodidae; B, ♂ gall of *Cyllindrococcus spiniferus*, Eriococcidae; C, ♂ gall of *Apiomorpha munita*, Eriococcidae; D, ♀ gall of same; E, ♀ gall, *Cyllindrococcus spiniferus*, Eriococcidae; F, *Pseudococcus longispinus*, ♀, Pseudococcidae; G, *Ceroplastes destructor*, ♀, Coccidae; H, *Parasaissetia nigra*, ♀, Coccidae; I–L, diaspidid scales, ♀♀: I, *Aonidiella aurantii*; J, *Berlesaspis spinifera*; K, *Chrysomphalus aonidum*; L, *Quadraspidiotus perniciosus*. [A, C–L by S. Monteith; B after Gullan 1984b]

Most of the described Australian species are endemic and cause little damage. *Symonicoccus* occurs on Cyperaceae and Poaceae, including sugar cane (Koteja and Brookes 1981). *Cryptes baccatus*, the wattle tick scale,

forms conspicuous aggregations on acacias, and many species in other genera encrust twigs and leaves. *Coccus hesperidum*, *Parasaissetia nigra* and *Saissetia coffeae* are introduced, cosmopolitan pest species of fruit trees

(Brimblecombe 1962; Brookes 1957, 1964; Hely *et al.* 1982). The greatest losses to crops result from sooty moulds growing on excreted honeydew making fruit unsaleable. Of six species of *Ceroplastes* present in Australia, *C. destructor* is of economic importance on citrus and *C. rubens* on many species of fruit trees (Brimblecombe 1956; Snowball 1969; Hely *et al.* 1982). *Pulvinaria elongata* occurs on sugar cane in Qld (D. J. Williams 1982). [Froggatt 1915; Zimmerman 1948; De Lotto 1965; Hamon and Williams 1984; M. L. Williams and Kosztarab 1972; D. J. Williams and Watson 1990]

20. Kerriidae (lac insects, Lacciferidae; Fig. 30.23F). This family, comprising more than 80 species, is distributed throughout the tropics with extensions into temperate areas. The family is distinctive, all species possessing brachial plates and a dorsal spine, and the anterior thoracic spiracles are much larger than the posterior pair. In Australia, *Austrotachardia*, *Kerria* and *Tachardina* colonise endemic trees and shrubs. In India and neighbouring territories the lac insect of commerce, *Kerria lacca*, is reared for its resinous secretions used for the production of shellac, sealing wax and other products. Lac insects contain the pigment laccaic acid. [Chamberlin 1923, 1925; Kapur 1958; Munting 1965, 1966; Varshney 1976]

21. Conchaspidae (Fig. 30.24E). This family is Afrotropical and Neotropical (Williams 1984) in distribution, with extensions into the Oriental Region. Females produce a white, usually circular and conical scale covering, sometimes resembling the scale of Diaspididae, but always lacking incorporated nymphal exuviae. Other diagnostic characters are the sclerotised, pointed abdomen fused into a pseudopygidium comprising the seventh and following segments. Antennae and legs are well developed, though tibia and tarsus are fused.

The only Australian representative is the tropicopolitan *Conchaspis angraeci*, known from *Boronia* (Rutaceae) in W.A. (Ben-Dov 1981). [Mamet 1954]

22. Halimococcidae (Fig. 30.24F). The family numbers just over 20 species world-wide. The hosts are Arecaceae and Pandanaceae and the family may be a relict of a larger one when palms were more widely distributed (D. J. Williams 1984). The posterior segments of the 2nd instar female are fused into a characteristic, dorsal, sclerotised operculum. The adult female is membranous and legless, and the posterior abdominal segments are fused into a simple pygidium. All species are pupillarial, i.e. the adult female remains within the exuviae of the previous (2nd) instar.

Two species are known from the Australian region, *Colobopyga australiensis* from Australia and *C. kewensis* from Lord Howe I. (Deitz 1979). [Stickney 1934; Beardsley 1963]

23. Diaspididae (armoured scales; Figs 30.21, 24G, 25I-L). Diaspididae are by far the largest and most successful coccoid family, numbering over 1700 species world-wide (Borchsenius 1966).

The adult female is legless and without antennae, and, normally, the fourth and following segments of the abdomen are fused and contracted to form a pygidium, which bears marginally a complex of tubular ducts,

marginal lobes, plates and gland spines (Ferris 1942). The common name refers to the wax-like, fibrous scale formed by and covering the insect. Scales are formed mainly with secretions from the pygidial complex, anal excreta and the exuviae of previous instars. Some species are pupillarial (Stoetzel 1976).

About 240 species are known from Australia, but the total number may eventually well exceed 1000. Most Australian species are endemic. *Maskellia globosa* is unusual in not producing an external scale, and in being a gall-former. Female nymphs induce the formation of gouty galls on the young twigs of *Eucalyptus*; male galls are horn-like and on leaves (Fuller 1897). Many of the introduced diaspidids are noxious (Brimblecombe 1962; Hudson 1967). Of the 43 principal diaspidid pest species of the world listed by Beardsley and González (1975), 24 are known from Australia. *Aonidiella aurantii* (California red scale) and *A. citrina* (yellow scale) are injurious to citrus (McLaren 1971; Willard 1972a, b). *Aphytis melinus* (HYMN: Aphelinidae) has been used very successfully in their biological control. *Quadraspidiotus perniciosus* (San José scale), *Q. ostreaeformis* (oyster shell scale), *Q. pyri* and *Q. lenticularis* attack pome and stone fruits (Brookes and Hudson 1969). [Rosen 1990, 1991; D. J. Williams and Watson 1990]

There is no general agreement on classification (Borchsenius 1966; Takagi 1969). A study of the distribution and form of the pygidial structures in the female is fundamental to the taxonomy of the Diaspididae (see Ferris 1942). Taxonomic studies of males have been made by Ghauri (1962) and of immatures by Howell (1980, 1984) and Takagi (1980). [Froggatt 1915-21b]

Suborder AUCHENORRHYNCHA

The monophyly of the Auchenorrhyncha (cicadas, spittle bugs, leafhoppers, planthoppers) is firmly established by the complex tymbal acoustic system and aristoid antennal flagellum characteristic of the group. The labium originates from the posterior region of the head, near to the occiput, no intervening sclerotic gula being present. The gut filter system may feature an encapsulating mid gut. All, except Cicadoidea, jump, and all have characteristic, elaborately spinose hind legs. Both wings, including venation, are well developed; venation is complete in the primitive cicada *Tettigarcta*; and secondary proliferation is common.

All are free living and phytophagous, mostly feeding in phloem and xylem tissue of angiosperms. Alary polymorphism is common, parthenogenesis extremely rare and viviparity unknown. [Pesson 1951; Strümpel 1983]

Infraorder CICADOMORPHA

The Cicadomorpha include all the non-fulgoromorph Auchenorrhyncha, namely Cicadoidea and the (saltatorial) Cercopoidea and Cicadelloidea. Head sulcated, not carinated; antennal pedicel not heavily sensoriated; mid coxae short, their bases close together; ambient vein usually present in fore and hind wing.

Superfamily CICAIDOIDEA

by M. S. MOULDS and M. CARVER

About 1200 species of Cicadoidea are known world-wide; they are most abundant in the tropics and subtropics. Most Australian species are endemic. Ocelli 3. Antennal flagellum usually 5-segmented, the segments progressively shorter and more slender. Tentorium complete. Fore femora usually thickened and spinous. Wing venation well developed.

Cicadas possess highly complex organs for the production and reception of sound; except in *Tettigarcta*, the sound-producing organs are present only in the male (Figs 2.30; 30.28). A pair of thin, exoskeletal, usually costate membranes, the tymbals, are situated dorsolaterally on each side of T1, and may be either exposed or partly or entirely concealed by tymbal covers, which are anteriorly produced folds of T2. Each tymbal is moved, internally, by a large tymbal muscle attached to it by a slender apodeme, and by a smaller, tensor muscle. Single or paired resonant air sacs derived from the tracheal system occupy much of the abdominal cavity. Sound is produced by the repeated, rapid contraction and relaxation of the tymbal muscles, causing repeated inward buckling of the tymbals, while the tensor muscles cause changes in curvature. Differences in tymbal structure and movement, air sac resonance, and associated abdominal movements are responsible for the variety and specificity of cicada calls.

Sound-receptor organs placed ventrally to the tymbals are present in both males and females. Except in *Tettigarcta*, they consist of a pair of large, mirror-like tympana, each one connected with groups of chordotonal sensilla within an auditory capsule. The tympana are con-

cealed beneath opercula, a pair of posteriorly produced, rigid, plate-like extensions of the thoracic venter. The opercula are adpressed to the abdomen, except during singing, when the abdomen is raised, forming a gap. The sounds (songs) are primarily for pair-forming, but may also promote aggregations of males, and repel predators.

Eggs are inserted in groups in oblique slits cut in branches or stems by the spear-like ovipositor. The newly-hatched nymph (*pronymph*) is still enclosed in its embryonic cuticle. Appendages remain adpressed, unbent, to the streamlined body and locomotion is restricted. The pronymph actively wriggles along to the exterior of the egg chamber, where it immediately moults to the free-limbed (1st) instar. These drop to the ground and burrow into the soil with their enlarged fore legs, which are also used to repel intruders from the moist air cell of compacted soil formed by each nymph near to plant roots. The nymphs of many species remain underground for several years. *Parnkalla muelleri* (yellow sugarcane cicada) and *Cicadetta crucifera* are unusual in having an annual life-cycle. There are usually five nymphal instars. The mature nymphs leave the soil when conditions are favourable and moult, often on nearby tree trunks or grass stems, usually after dusk.

Cicadas are mostly xylem-feeders; their excreta are consequently watery and often profuse. Nymphs of *P. muelleri* and *Cicadetta crucifera* occasionally damage sugar cane.

Because of the extent of the differences separating *Tettigarcta* from all other cicadas, only two families are recognised here. Other arrangements have been used by Boulard (1976) and Duffels and van der Laan (1985). [Pringle 1957; Metcalf 1962-63; Wade 1964; Claridge 1985; Moulds 1990]

Key to the Families and Subfamilies of Cicadoidea Known in Australia

1. Radial sector (RP) arising near base of fore wing and veins CuP and 1A separated in fore wing (Fig. 30.4E); distance between eyes from dorsal aspect less than their diameter; pronotum long, overreaching mesonotum (Fig. 30.26) **Tettigarctidae**
 RP arising from node, near or beyond middle of costal margin; veins CuP and 1A concurrent for most of their length (Fig. 30.4F); distance between eyes in dorsal view greater than their diameter; pronotum shorter, not overreaching mesonotum (Fig. 30.27) **Cicadidae**. 2
- 2(1). ♂ with tymbal covers present, completely or partly covering the tymbal cavities (Fig. 30.28A) **CICADINAE**
 ♂ with tymbal covers absent, the tymbals thus completely exposed **TIBICININAE**

24. Tettigarctidae (Figs 30.4E, 26). This family is also known as Mesozoic and Tertiary fossils in the Northern Hemisphere. The sole living representatives, *Tettigarcta crinita* and *T. tomentosa*, are confined largely to high altitudes in south-eastern mainland Australia and Tas. respectively. Unlike all other cicadas, tymbals and associated muscles are present in both sexes although less well developed, and resonant air sacs are absent. Tympana are absent, but chordotonal organs associated with thinned cuticle on either side of S2 are presumably acoustic receptors (Pringle 1957). *Tettigarcta* differs from other cicadas in many other features. The fore wing venation is complete and the nodal line, which allows the apical half of the wing to flex downwards in flight, is conspicuously

developed. The insects are heavily pilose, the thoracic nota are conspicuously posteriorly produced, fore femora not markedly swollen or spinous, pretarsal empodia present, parameres present in male, and thoracic ganglia primitively discrete.

Adults are crepuscular, remaining hidden during daytime, often under bark. They are most common in late summer and early autumn, and tolerate subzero temperatures. Nymphs feed on *Eucalyptus* roots. [J. W. Evans 1941]

25. Cicadidae (Plate 3, G; Figs 30.4F, 6D, 9A, 10C, D, 27, 28). All but four of the Australian species of this large, cosmopolitan family are endemic, as are 28 of the 38 Australian genera. Many species inhabit arid regions,



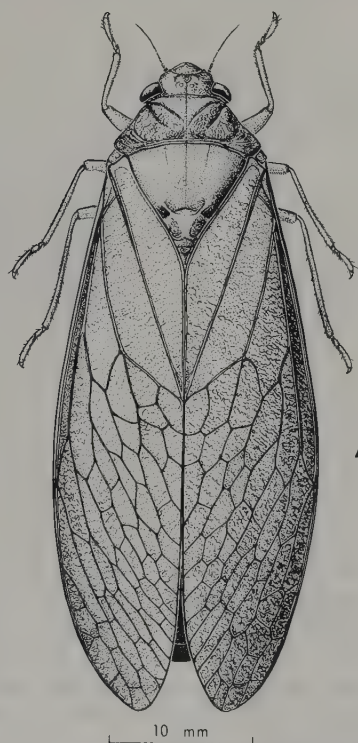
A



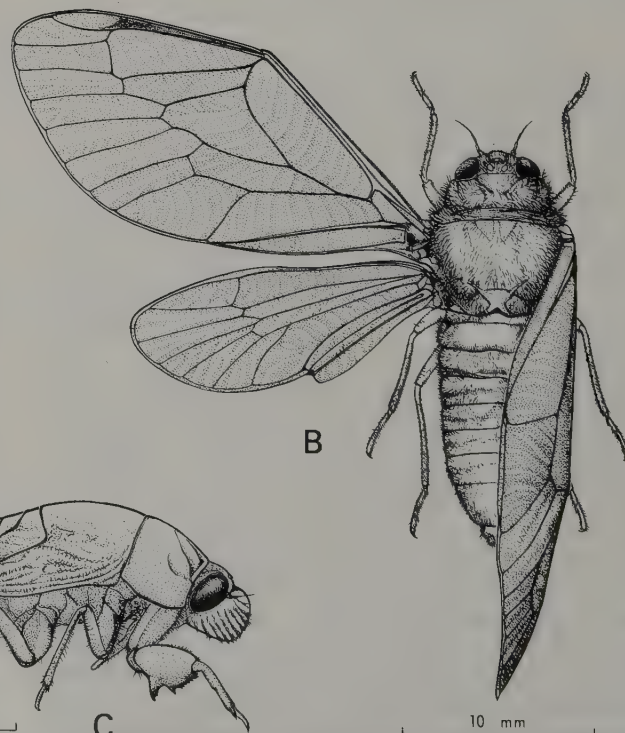
B

Fig. 30.26 Tettigarctidae: A, *Tettigarcta crinita*; B, *Tettigarcta tomentosa*.

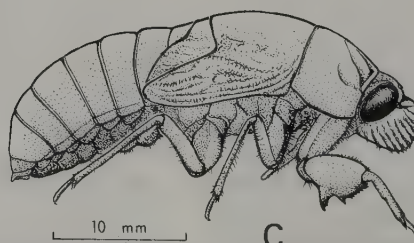
[A by S. P. Kim; B by S. Monteith]



A



B



C

Fig. 30.27 Cicadidae: A, *Cystosoma saundersii*, ♂; B, *Froggattoides typicus*; C, *Macrotristria angularis*, nymph.

[S. Monteith]

commonly breeding on grasses, the adults appearing after heavy rains. The CICADINAE (70 spp.) include mostly large species, almost half belonging to *Macrotristria* and *Psaltoda*. The greengrocer or yellow Monday, *Cyclochila australasiae*, is a common species in suburban Sydney and Melbourne. *Arunta* (2 spp.) and *Thopha* (3 spp.) males have spectacular dome-like tymbal covers. The latter are known as double drummers. The TIBICININAE (180 spp.) contain mostly small (*Urabunana*) to medium-sized cicadas. Many species are included in *Cicadetta*, which is also well represented in the Holarctic region; a few exhibit sexual dimorphism, a rare feature in cicadas. In some Australian genera, the abdomen of the male is unusually inflated, the most bizarre example being the bladder cicada, *Cystosoma saundersii* (Fig. 30.27A), which is normally green or orange yellow, with concolorous leaf-like wings. *Froggattoides typicus* (Fig. 30.27B) inhabits arid and semi-arid regions and its strongly bent fore wings may have a stridulatory function. *Abricta* spp. characteristically face downwards when at rest; *A. curvica* is the floury baker.

Superfamily CERCOPOIDEA

by M. J. FLETCHER, J. W. EVANS and M. CARVER

Many cercopoids, known as froghoppers or spittle bugs, superficially resemble cicadelloids or leafhoppers, but may be distinguished by the characters given in the key. They differ also in fore wing venation, and in the biology and associated adaptive structures of their nymphs. Head variously shaped, sometimes narrowly produced anteriorly; tentorium complete; paired ocelli, when present, always on the crown. Fore wing usually with short Sc; M usually, though not invariably, basally incorporated in the same vein as CuA, and never proximally associated with R; base of wing with ventral flange; hind wing with M unbranched. Hind coxae short, conical, laterally dilated.

Nymphs of Cercopidae and Aphrophoridae live enclosed in spittle (Fig. 30.29A) either subterraneously (many Cercopidae) or above ground (Aphrophoridae). Nymphs of Machaerotidae inhabit calcareous tubes or cases (Figs 30.29B, C), which are the product of the Malpighian tubules, and in which they live and feed immersed in their liquid excreta. Nymphs of all families have a ventral abdominal channel, which terminates anteriorly near the openings of the large mesothoracic spiracles. In spittle-making species this channel is tubular, the abdominal terga being curved ventrally below the venter to meet in mid-line. In the case-making machaerotids, it is permanently closed by a membrane. Spittle is formed by air being taken into the ventral abdominal channel and expelled posteriorly through a film of anal excreta, thus forming bubbles. In some Machaerotidae T5 and T6 are modified so as to form an operculum with which the

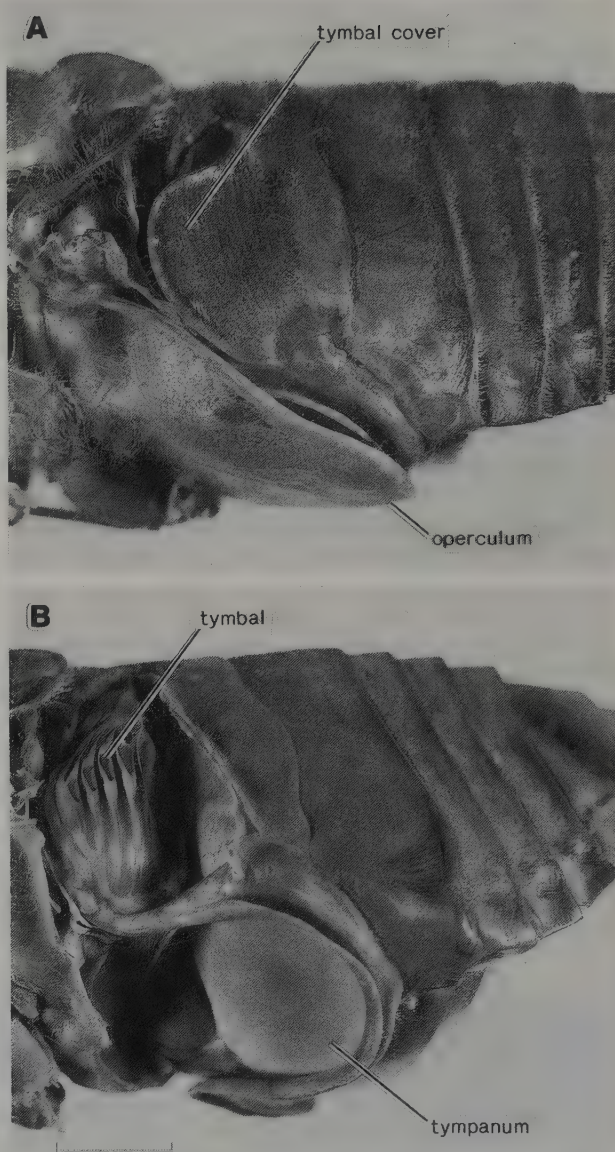


Fig. 30.28 *Cyclochila australasiae*, ♂, Cicadidae. A, lateral view of abdomen, to show tymbal cover and operculum; B, ventrolateral view, with tymbal cover and operculum removed, to show tymbal and tympanum. Scale = 5 mm. [J. P. Green]

opening of the tube can be closed (Fig. 30.29C). Spittle and case formation presumably protect against desiccation and predation (J. W. Evans 1940; Marshall 1966; Marshall and Cheung 1973).

The Aphrophoridae and Machaerotidae are treated as subfamilies of Cercopidae by some authors (Ossiannilsson 1981; Hamilton 1982). Metcalf (1960–62) and Wade (1963) catalogued the world species. [J. W. Evans 1966]

Key to the Families of Cercopoidea Known in Australia

1. Hind margin of pronotum straight or slightly curved in mid section (Fig. 30.30A); eyes, in dorsal view, usually circular **Cercopidae**
- Hind margin of pronotum W-shaped (Figs 30.30B, C); eyes, in dorsal view, elongate or ovate 2
- 2(1). Fore wing with a wide appendix (peripheral membrane) continuing around its apex (Fig. 30.30E); pronotum convex;

- hind wing with R unbranched, only 1 cell between M and costal margin **Machaerotidae**
 Fore wing without or with a very small appendix; pronotum flat, sometimes anteriorly declivous; hind wing with once-branched R, 2 cells between M and costal margin **Aphrophoridae**

26. Cercopidae (Plate 3, F; Figs 2.43; 30.29A, 30A). World-wide, richly represented in the tropics, and including the largest and most handsome cercopoids. The largest species in Australia is *Megastethodon urvillei*, up to 19 mm in length, which is found in north-eastern Australia and New Guinea. The smaller, orange and black *Aufidus trifasciatus* is also restricted to northern Australia and further north. *Euryaulax carnifex* infests sugar cane. *Petyllis deprivata*, brown with gold pubescence, has a wide distribution, and *Tonnoiria* spp. occur in Tas. and at high altitudes on the mainland. [J. W. Evans 1966]

27. Aphrophoridae (Figs 30.30B, D). The largest family of the Cercopoidea and cosmopolitan, although poorly represented in Australia. The two most abundant and widely distributed Australian species are *Philagra parva*, which has a long, narrowly produced head and is associated particularly with *Casuarina* and *Acacia*, and *Bathylus albicinctus* which is beetle-like, brown and white, and feeds on numerous plants. *Anyllis leiala* is common on *Eucalyptus* in eastern Australia. [J. W. Evans 1966]

28. Machaerotidae (Figs 30.29B, C, 30C, E). Restricted to tropical Africa, the Oriental Region and Australia. The most frequently encountered Australian species are *Chaetophyes compacta*, with shiny and seemingly crumpled fore wings, and *Pectinariophyes stalii*. Both belong in ENDERLEINIINAE. The MACHAEROTINAE are represented by *Machaerota* (2 spp.; in northern Australia) in which

the scutellum is considerably enlarged and produced posteriorly into a spine-like process. [J. W. Evans 1940, 1970; Maa 1963a; Marshall and Marshall 1966]

Superfamily CICADELLOIDEA

by M. J. FLETCHER, J. W. EVANS and M. CARVER

A large diverse superfamily, represented in Australia by the cosmopolitan Cicadellidae, the predominantly Australian Eurymelidae, and the Membracidae, which are largely Neotropical. Leafhoppers and treehoppers differ from other Auchenorrhyncha in having a reduced tentorium, in venational features, in the transverse hind coxae, in the armature of the hind tibiae, and in having broad pretarsal claws. Feed in xylem or phloem, less commonly in parenchyma. Hosts almost exclusively angiosperms; the Australian species feed predominantly on trees and shrubs, although some are obligate grass feeders or root-feeders.

The classification of J. W. Evans (1977) is followed here. Eurymelidae retain family status and Membracidae are retained in Cicadelloidea. Other arrangements have been proposed by H. H. Ross (1957), Strümpel (1972) and Hamilton (1983). Metcalf (1962–68), Metcalf and Wade (1963–65) and Burnside (1971) catalogued the world species. Knight and Nielsen (1986) listed all extant subfamily and tribal names in the Cicadellidae. [J. W. Evans 1966; DeLong 1971; Nault and Rodriguez 1985]

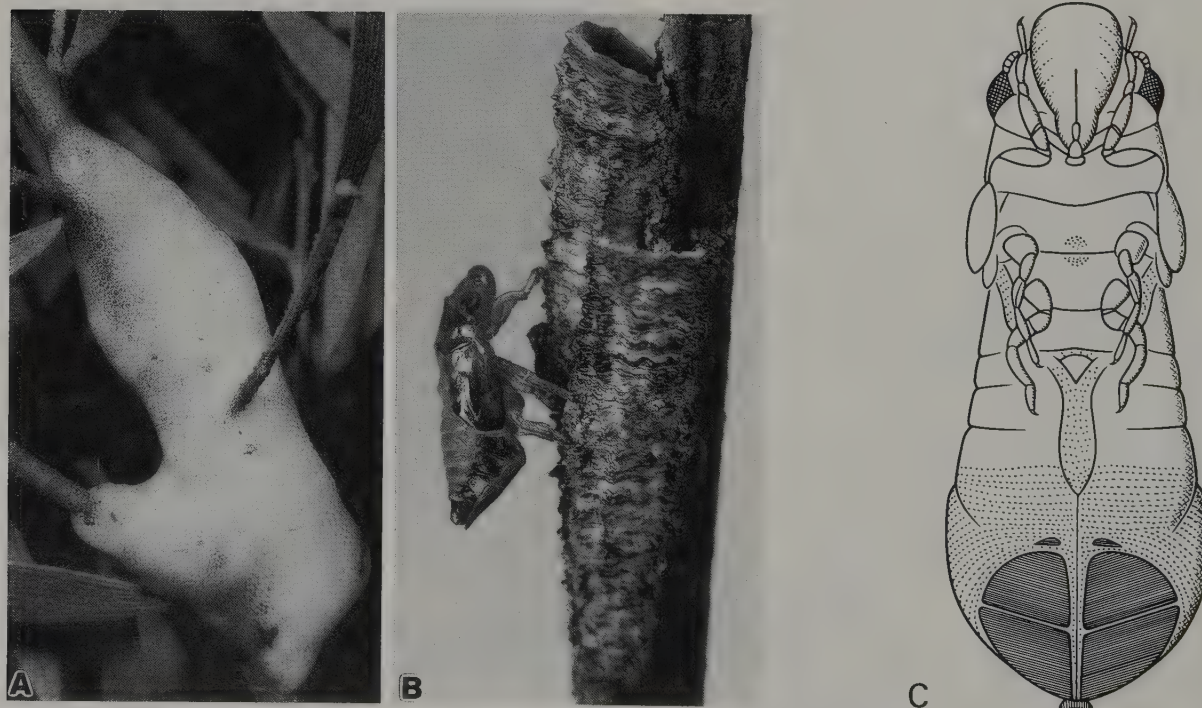


Fig. 30.29 A, 'spittle' of nymphs of Cercopidae; B, dwelling tubes and nymph of *Chaetophyes* sp., Machaerotidae; C, machaerotid nymph with operculum, ventral aspect.
 [A, B by P. L. Grant, C. Lourandos; C after J. W. Evans 1940]

Key to the Families of Cicadelloidea Known in Australia

1. Pronotum considerably enlarged, sometimes grotesque (Fig. 30.36) **Membracidae**
 Pronotum usually of normal proportions; if enlarged, then scutellum completely exposed 2
- 2(1). Fore wing with M_{1+2} extending to apex, RP absent (Fig. 30.4H); base of aedeagus attached dorsally; hind tibiae, except in myrmecophiles, with 1 or several spines on prominent bases (Fig. 30.31B); ocelli on face distant from the apical margin (Fig. 30.34) **Eurymelidae**
 Fore wing usually with M_{1+2} apically fused with RP (Fig. 30.4G); base of aedeagus attached ventrally; hind tibiae with numerous spines (Figs 30.31C, D), which are not on prominent bases, except in most Ledorinae, which have ocelli dorsal, marginal or on the face near apical margin **Cicadellidae**

29. Cicadellidae (leafhoppers; Figs 30.1A, B, 4G, H, 31A, C-E, 32, 33; 36.7C). The Australian fauna is rich, with an unusually high proportion of arboreal species. M. J. Fletcher and Stevens (1988) provided a key to the Australian subfamilies and tribes.

Three of the five tribes of ULOPINAE are represented in Australia. Ulopini, which comprise relict forms, have maxillary plates separated from the genae by a transverse

suture. Cepheleini, which occur also in South Africa and New Zealand, include forms resembling long, narrow, plant seeds. All known Ulopini and Cepheleini show alary dimorphism. The brachypterous *Myerslopella* is the sole Australian representative of Myerslopiini, distinctive in having pronotal paranota. [J. W. Evans 1968, 1977]

Of the LEDRINAE, Stenocotini and Thymbrini are endemic. The third tribe, Ledorini, is widely distributed

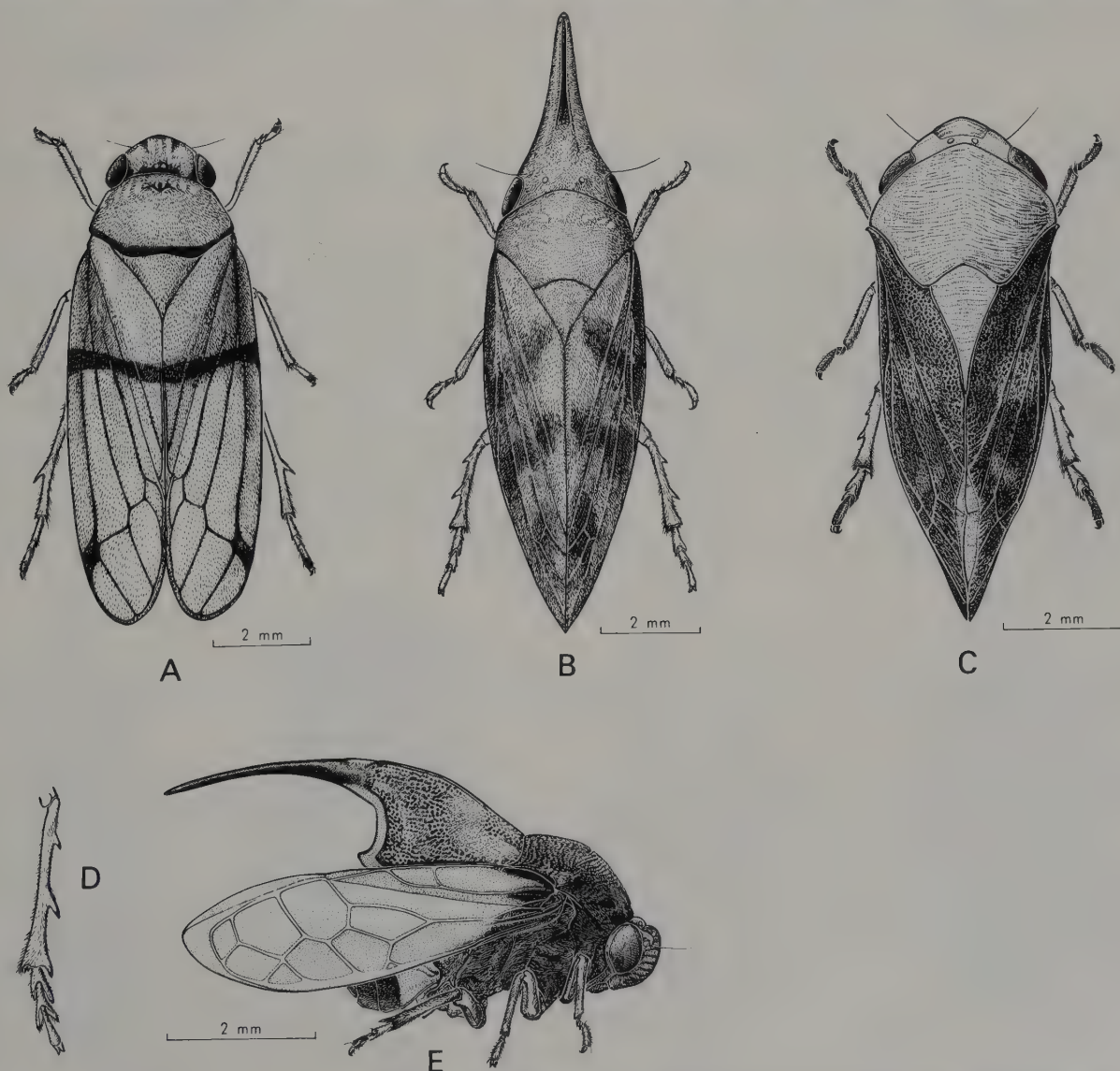


Fig. 30.30 A, *Auidus trifasciatus*, Cercopidae; B, *Philagra parva*, Aphrophoridae; C, *Chaetophyes compacta*, Machaerotidae; D, hind tibia and tarsus of *P. parva*; E, *Machaerota finitima*, Machaerotidae. [S. Monteith]

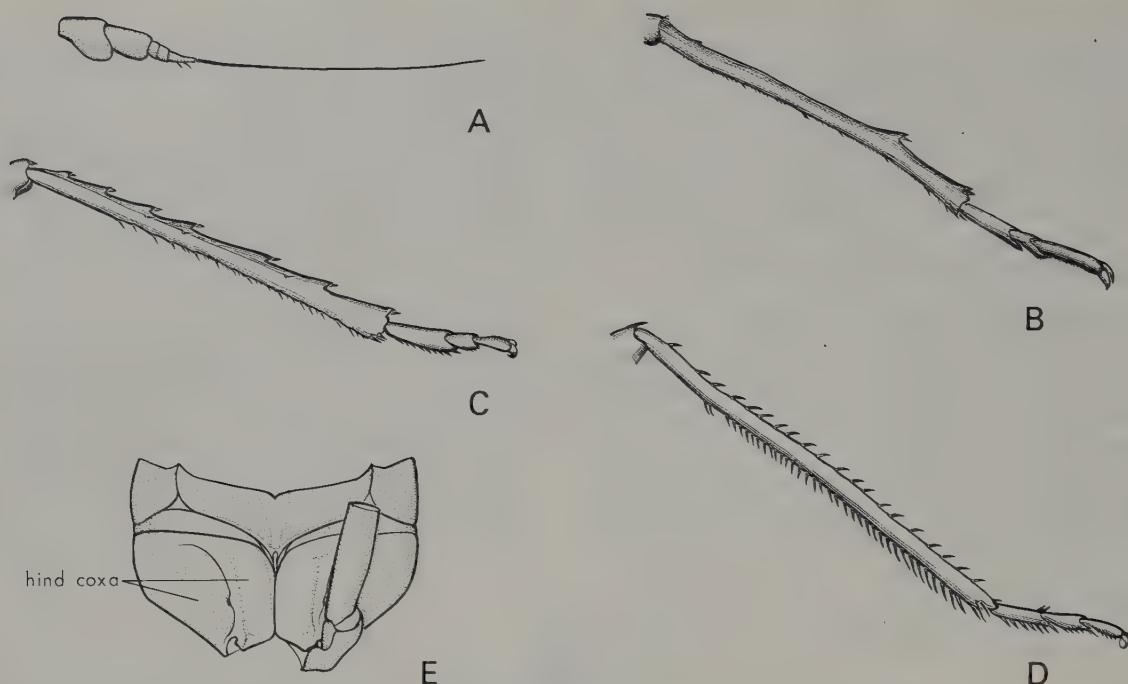


Fig. 30.31 A, antenna of *Stenocotis depressa*, Cicadellidae; B, hind tibia and tarsus of *Eurymela fenestrata*, Eurymelidae; C, same of *Stenocotis depressa*, Cicadellidae-Ledrinae; D, same of *Cofana spectra*, Cicadellidae-Cicadellinae; E, ventral aspect of metathorax of *C. spectra*. [S. Monteith]

(J. W. Evans 1969). *Ledromorpha planirostris* (Ledrini) is the largest Australian leafhopper (23–28 mm long) and is apparently parthenogenetic. Stenocotini, of which the best known is *Stenocotis*, have wafer-thin nymphs frequently found on *Eucalyptus* trunks. *S. depressa* is sexually dimorphic and bears ocelli in lateral pits on the anterior margin of the spatulate head. The largest Thymbrini, *Rhotidus*, is brown, with a triangular head.

EUACANTHELLINAE comprise one species of *Euacanthella* from Australia and one from New Zealand. They occur in marshy habitats.

CICADELLINAE, which are most abundant in the

Neotropical Region, are represented in Australia by small, bluish-black and yellow *Ishidaella*, by the tropicopolitan *Cofana spectra*, and by a few species confined to north-eastern Qld. Keys to genera of Cicadellini have been provided by Young (1977, 1986). The NIRVANINAE are essentially Oriental. The Australian species are found in Qld, with a few exceptions such as *Occinirvana eborea* on *Casuarina* in W.A.

MACROPSINAE are cosmopolitan, and are exceptionally well represented in Australia (J. W. Evans 1971b). *Stenoscopus drummondi* (7 mm) is the largest known macropsine and *Stenopsoides turneri* has an enlarged

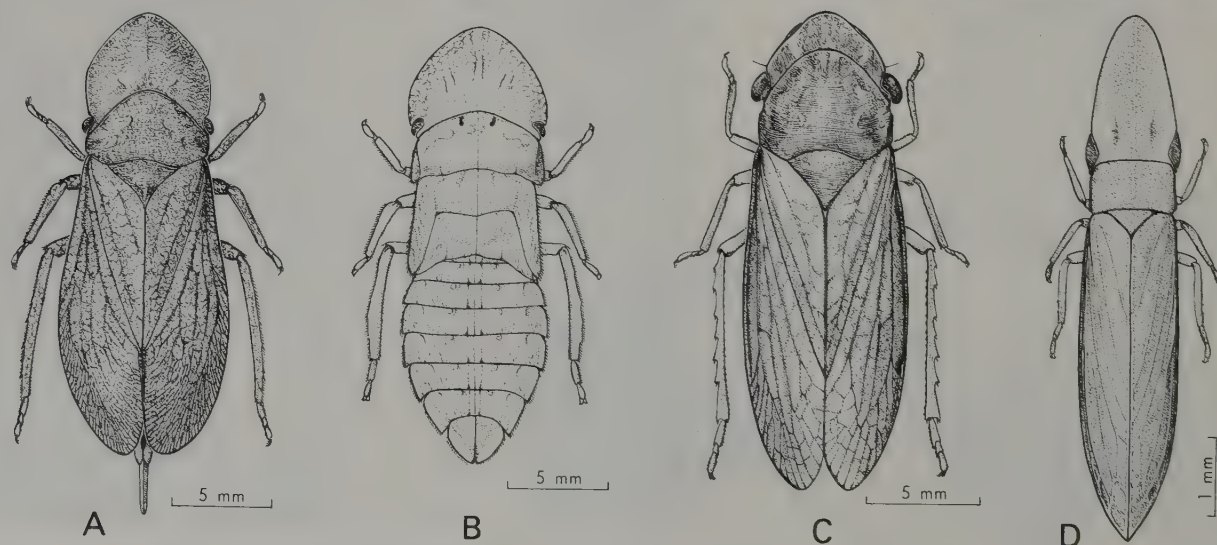


Fig. 30.32 Cicadellidae: A, *Ledromorpha planirostris*, Ledrinae; B, nymph of same; C, *Stenocotis depressa*, Ledrinae; D, *Cephalelus ianthe*, Ulopinae.

[S. Monteith]

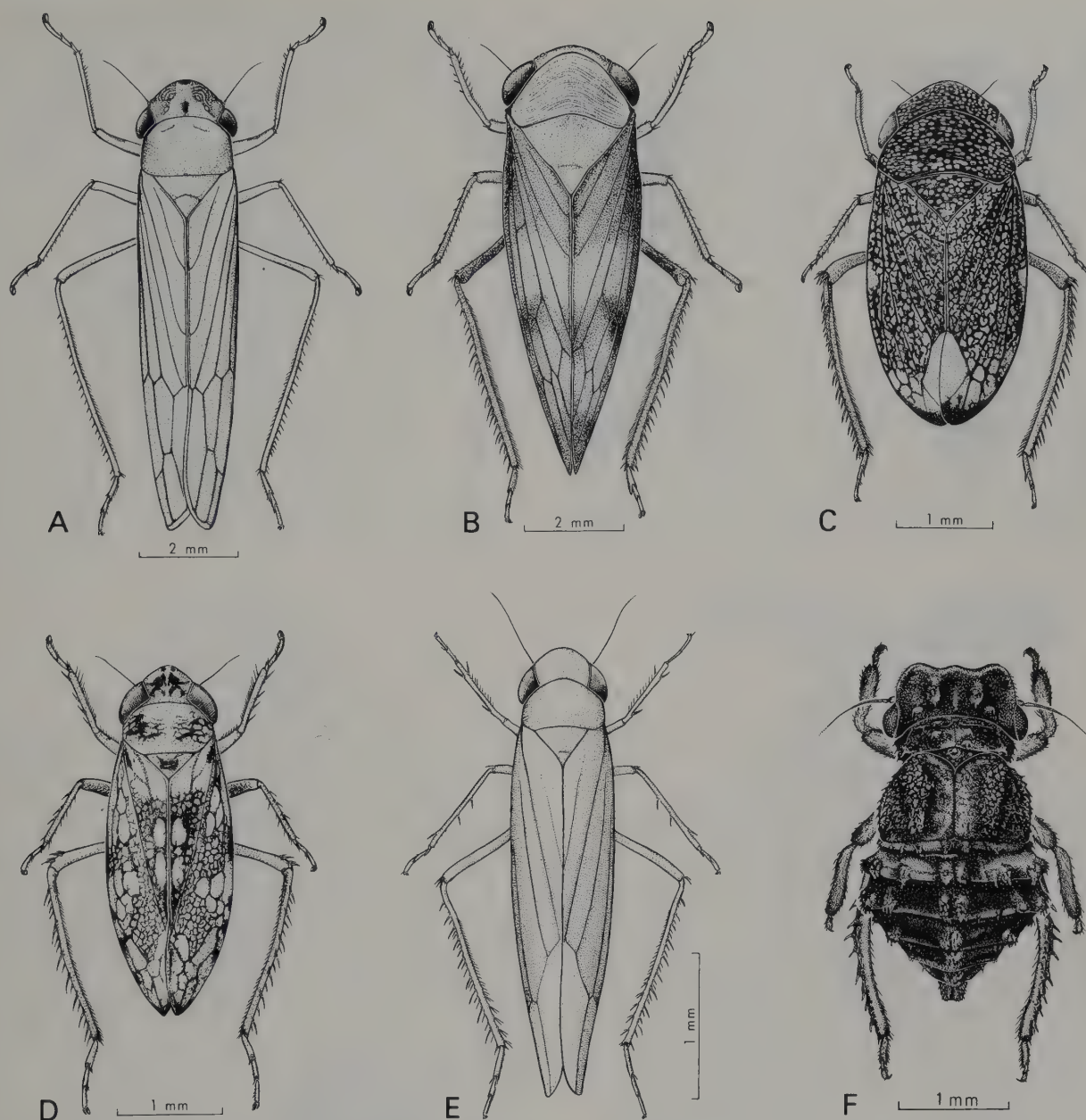


Fig. 30.33 Cicadellidae: A, *Cofana spectra*, Cicadellinae; B, *Brunotartessus fulvus*, Tartessinae; C *Neovulturnus vaedulcis*, Penthimiinae; D, *Orosius argentatus*, Deltocephalinae; E, *Zygina zealandica*, Typhlocybinae; F, *Myerslopella* sp., Ulopinae. [A–E by S. Monteith; F by G. Thompson]

pronotum, which is narrowly produced in front of the head. Both are confined to south-western Australia. A key to world genera and subgenera has been provided by Hamilton (1980).

The large, cosmopolitan AGALLIINAE are represented in Australia by *Austroagallia torrida*, which transmits rugose leaf curl in *Malva*, *Datura* and red clover. The endemic AUSTRAGALLOIDINAE comprise only *Austroagalloides* (8 spp.), species of which live on *Eucalyptus* and exhibit marked sexual dimorphism. Superficially they resemble the widespread IDIOCERINAE, which are abundantly represented in Australia, particularly by *Rosopaella* on *Eucalyptus* and *Melaleuca* (Webb 1983). The tropicopolitan COELIDIINAE are represented by

only a few *Tharra* species in north-eastern Qld; they have unusually long antennae and a somewhat fulgoroid appearance. Of the 38 described genera of TARTESSINAE, 18 are indigenous to Australia, and another 4 have a wider range (F. Evans 1981). They are generally associated with xerophytic trees, but some live in Qld rainforest.

Three tribes of IASSINAE are known in Australia. The cosmopolitan Iassini are represented by *Batracomorphus* (18 spp.) (Knight 1983). *B. angustatus* transmits plant mycoplasma diseases in Australia (Grylls 1979). Trocnadini and Reuplemmelini are endemic and are separable from Iassini by head shape and ocellar position. The PENTHIMIINAE are a seemingly diverse group. Some, like *Neodartus* and *Vulturnus*, are largely confined to north-

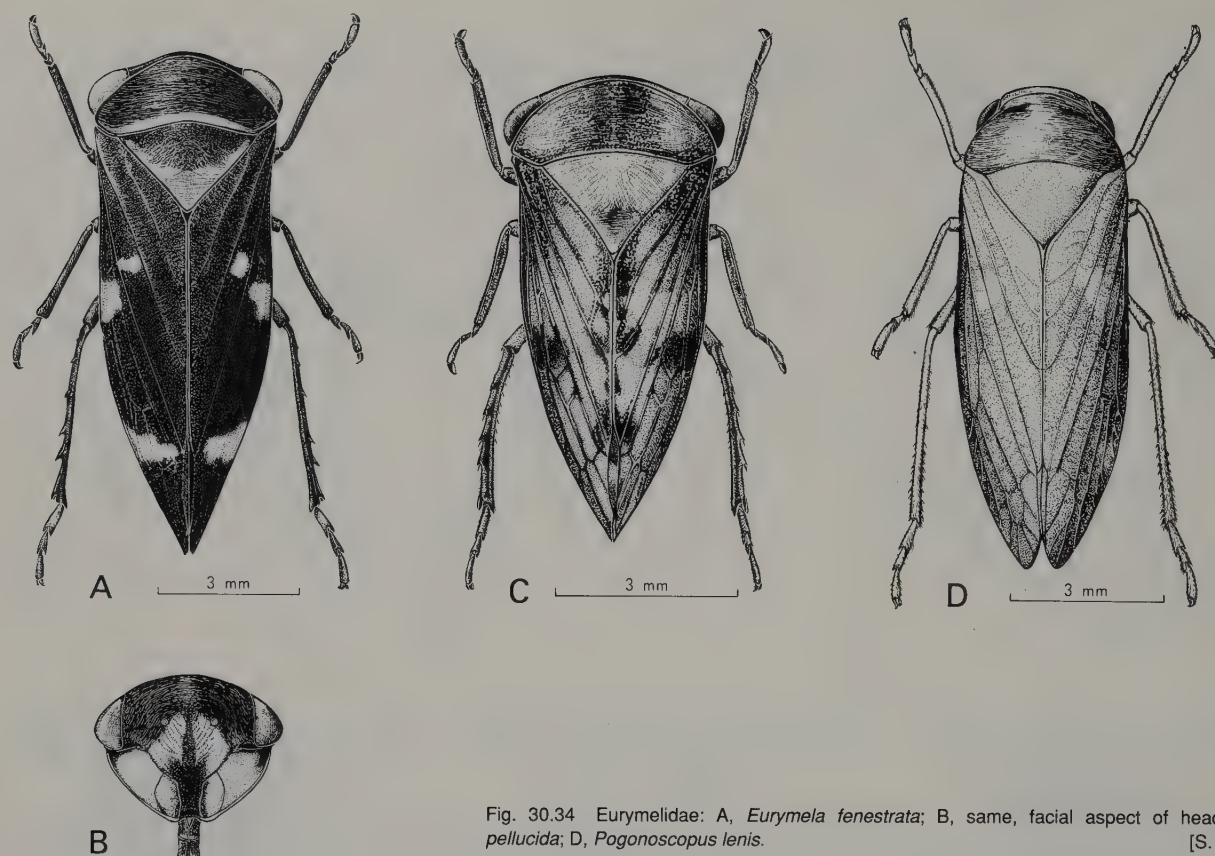


Fig. 30.34 Eurymelidae: A, *Eurymela fenestrata*; B, same, facial aspect of head; C, *Ipo pellucida*; D, *Pogonoscopus lenis*. [S. Monteith]

eastern Qld; others, such as *Ectopiocephalus australis* and *Chinaella* spp. occur inland in arid areas (J. W. Evans 1972). [J. W. Evans 1966]

DELTOCEPHALINAE are most abundant in the Nearctic Region. Most Australian species belong to cosmopolitan genera and may be of comparatively recent establishment. An example is *Orosius argentatus* (Euscelini), a well-known vector of plant mycoplasma diseases in Australia (Grylls 1979). Macrostelini are minute to small, yellow or green, and with reduced fore wing venation. They are represented in Australia by the cosmopolitan *Balclutha* and *Cicadulina* and the predominantly Oriental *Nesoclutha*; a few species are known vectors of virus diseases of cereals in Australia (Grylls 1979). The few Australian Hecalini are tropical grass-feeders. Paradorydiini are mostly small, narrow and elongate, superficially resembling the seed-

like Cephalini (Ulopinae) but with marginal instead of dorsal ocelli.

PARABOLOPONINAE are represented by *Dryadomorpha* (2 spp.) (Webb 1981). XESTOCEPHALINAE are small, oval and brown with yellowish markings and myrmecophilous; they are represented by *Xestocephalus* (5 spp.) and *Myrmecophryne formiceticola*. TYPHLOCYBINAE are very small, coloured and with reduced fore wing venation. They resemble some deltocephaline Macrostelini but Australian species lack a fore wing appendix. Many species cause leaf speckling, notably the exotic *Edwardsiana crataegi* on apple and hawthorn and *Ribautiana ulmi* on elms. Lower (1952) reviewed Australian *Austroasca* and Dworakowska (1972) described Australian species of Dikraneurini, but otherwise the subfamily has been little studied in Australia.

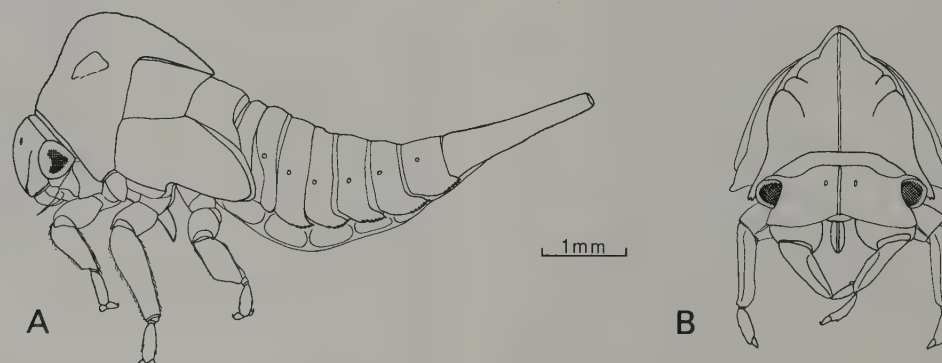


Fig. 30.35 *Sextius virescens*, Membracidae, final instar nymph.

[After Kitching and Filshie 1974]

30. Eurymelidae (Plate 3, H; Figs 3.28; 30.4H, 34). The family is confined to Australia, New Guinea and New Caledonia. Many species are brightly coloured, or predominantly black; the largest belong in *Eurymela* and *Eurymelops*. Male genitalia are distinctive; the aedeagus is dorsally situated and lacks association with the parameres; in cicadellids and membracids it is basally continuous with a connective joining the parameres. Most are readily recognisable by their widely flattened face with the ocelli immediately in front of the diamond-shaped frontoclypeus. Most feed on *Eucalyptus*, some on other plants, especially *Casuarina*. The nymphs, especially, are gregarious and do not jump if disturbed. Unlike most cicadellids, eurymelids are always ant-attended and some *Pogonoscopus* and related genera live in ant nests. [J. W. Evans 1931, 1946–47, 1966]

31. Membracidae (treehoppers; Figs 30.35, 36). The enlarged and often bizarrely shaped pronotum is the most characteristic feature of the Membracidae.

The commonest species, *Sextius virescens*, is green and, like many other Australian membracids, feeds on

Acacia. *Eufairmairia gigantica* may reach 12 mm in length. *Acanthucus* has a narrow, elevated median pronotal process in addition to the usual lateral ones. *Sertorius australis* has a convex pronotum bearing very small acute lateral processes. The most bizarre species are *Lubra spinicornis* and *Eutryonia monstriifer*.

The nymphs are ant-attended and usually gregarious. The abdomen is upturned, and the 10th or anal segment retractable into the long and tubular T9. Kitching and Filshie (1974) described the morphology and mode of action of the anal apparatus of *Sextius* nymphs. [J. W. Evans 1966]

Infraorder FULGOROMORPHA

The Fulgoromorpha comprise the single superfamily Fulgoroidea, containing 20 recognised families, of which 14 are represented in Australia. The monophyly of the group is firmly established by several synapomorphies including a sensoriated antennal pedicel, facial carinae, absence of ambient vein in hind wing and an anterior diverticulum of mid gut.

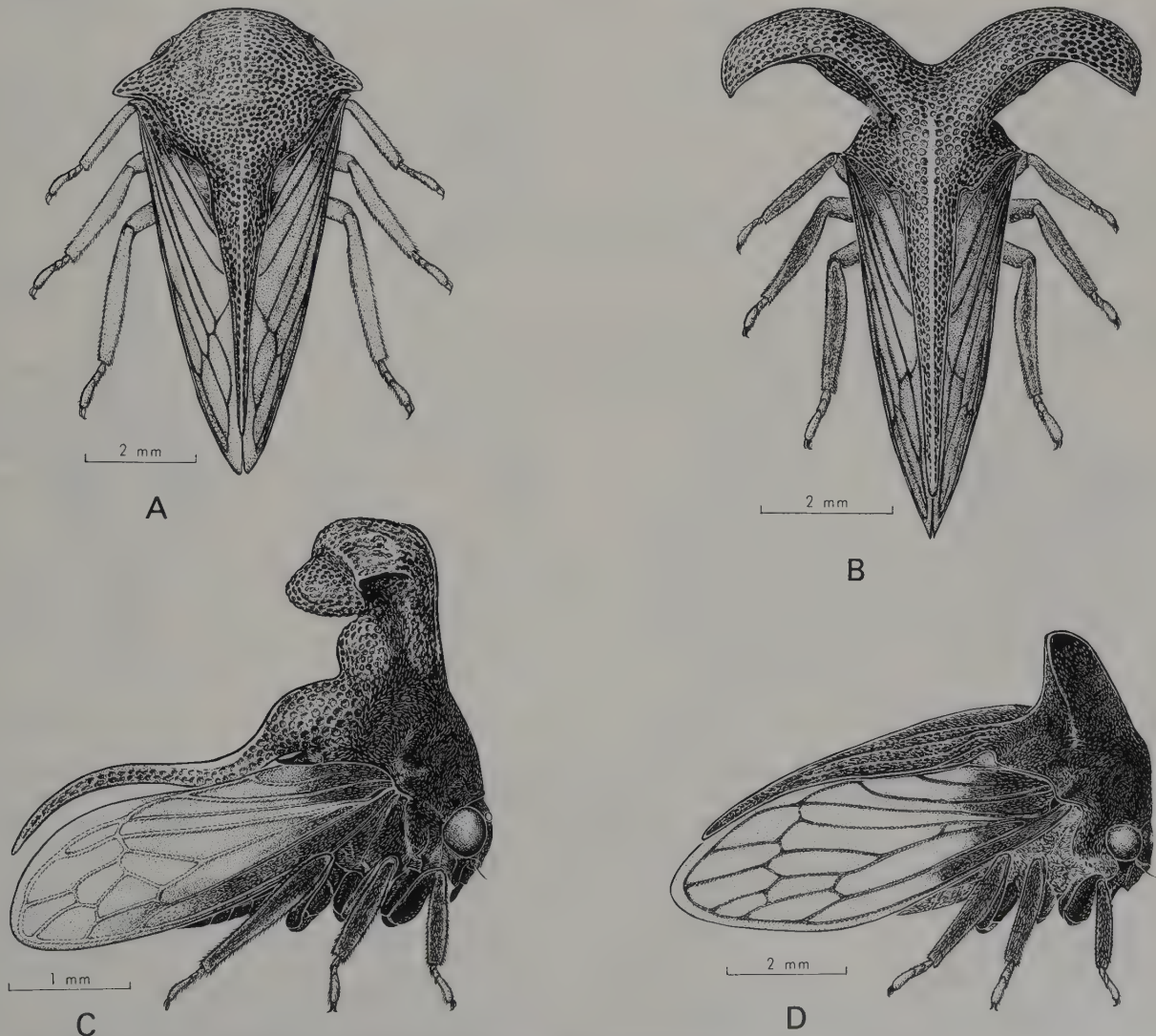


Fig. 30.36 Membracidae: A, *Sertorius australis*; B, *Eufrenchia falcata*; C, *Eutryonia monstriifer*; D, *Eufairmairia fraternus*.

[S. Monteith]

Superfamily FULGOROIDEA

by M. J. FLETCHER and M. CARVER

Very diverse planthoppers. Clypeus not extending to between the eyes in adults, and distinct from frontal region. Head divided by carinae not sutures. Antennae situated beneath eyes, with an enlarged, densely sensoriated pedicel. Ocelli 2, occasionally 3, the lateral ocelli on the sides of the face adjacent to eyes and antennae. Tegulae present on mesothorax (except in brachypterous dictyopharids). Anal veins of fore wing apically confluent; hind wing without an ambient vein. Mid coxae long, the

bases widely separated. Wax plates common in females, producing wax to cover eggs; wax production common in nymphs, often in the form of long abdominal filaments. Nymphs also with abundant sensory pits.

Fulgoroidea are largely tropicopolitan. Their biology is not well known. Not highly host-specific; usually phloem-feeders on angiosperms, though some Achilidae and Derbidae are mycetophagous. Gut filter system present. The world species were catalogued by Metcalf (1932–58) and Wade (1960); more than 10 000 have been described. [Nault and Rodriguez 1985]

Key to the Families of Fulgoroidea Known in Australia

1. Hind tibiae with a large movable spur at apex (Figs 30.37A, B, 38) **Delphacidae**
Hind tibiae without a large movable spur (Figs 30.37C–E) 2
- 2(1). Apex of 2nd segment of hind tarsi truncate or emarginate, with a ventral row of 3 or more small dark spines (Fig. 30.37C) 3
2nd segment of hind tarsi small, apex rounded or pointed, without spines (Fig. 30.37E), or with only one at each side (Fig. 30.37D) 8
- 3(2). One or both anal veins of fore wing granulate (Fig. 30.41D); apical segment of rostrum much longer than wide **Meenoplidae**
Anal veins not granulate, or, if so, granules small, similar to those on other veins; or apical segment of rostrum short, about as long as wide 4
- 4(3). Clavus open distally, running full length of fore wing, with numerous cross-veins between anal veins; anal area of hind wings reticulate. [Large species, 15 mm or more in length; clypeus with lateral carinae; head often prolonged] (Figs 30.39B, C) **Fulgoridae**
Clavus closed distally, or, if open, without numerous cross-veins between anal veins; anal area of hind wings not reticulate 5
- 5(4). Apical segment of rostrum short, almost as wide as long (Fig. 30.37H) **Derbidae**
Apical segment of rostrum distinctly longer than wide (Fig. 30.37G) 6
- 6(5). Apex of confluent anal veins of fore wing reaching apex of clavus (Fig. 30.5A) [usually horizontally flattened forms with membranes overlapping] **Achilidae**
Apex of confluent anal veins not reaching apex of clavus 7
- 7(6). Head prolonged in front, or, if not, frons with 2 or 3 carinae (in addition to lateral carinae) (Figs 30.37I, 41F, G), or the tegulae absent and claval furrow of fore wing obscure; median ocellus absent **Dictyopharidae**
Head usually not prolonged; if prolonged, frons with only a median carina or none (excluding lateral margins) (Fig. 30.37J); tegulae and claval furrow always distinct (Fig. 30.39A); median ocellus sometimes present. [Fore wing veins often bearing setae set in tubercles] **Cixiidae**
- 8(2). Apex of 2nd segment of hind tarsus with a spine at each side. [Anal vein of fore wing nearly always ending at apex of clavus] 9
Apex of 2nd segment of hind tarsus without spines 12
- 9(8). Posterior angle of mesonotum separated from the rest of the mesonotum by a groove or fine line and at same level as main anterior division (Fig. 30.37K); fore wing usually with evident nodal line; cross-veins more numerous in distal than in basal part (Fig. 30.40) **Tropiduchidae**
Posterior angle of mesonotum not so separated (Fig. 30.37L) or, if so, by a broad trough and at different level from main anterior division; fore wing with or without an evident nodal line, but cross-veins not restricted to distal part of wing 10
- 10(9). Fore wing clavus with conspicuous granules (Figs 30.41B, 44) **Flatidae**
Clavus without granules 11
- 11(10). Costal margin of fore wing more or less evenly convex throughout; antennae usually clearly separated from lower margin of eye; wings usually transparent and tectiform, sometimes reduced or strap-like (Fig. 30.41H) **Nogodinidae**
Costal margin of fore wing strongly convex or lobed at base, thence weakly convex to apex; antennae often close to lower margin of eye; fore wings opaque or heavily marked with dark brown, usually convex and sometimes elytri-form (Fig. 30.42) **Issidae**
- 12(8). Frons longer than wide; clypeus with lateral carinae; frons usually with carinae in addition to carinate margins [Fig. 30.45] **Lophopidae**
Frons wider than long; clypeus without lateral carinae; median carina usually absent from frons 13
- 13(12). Lateral margins of frons rounded or undulate, not angulate; precostal area of fore wing as wide as or wider than costal cell throughout (Fig. 30.41A) [fore wing often triangular, costal and apical margins subequal and clavus reaching nearly to apical margin] **Ricaniidae**

Lateral margins of frons outwardly angulately produced at or near level of antennae (Fig. 30.43); precostal area, if present, narrower than costal cell distally and greatly narrowed in proximal half [fore wing never triangular, apical margin shorter than costal margin, clavus not as above] **Eurybrachyidae**

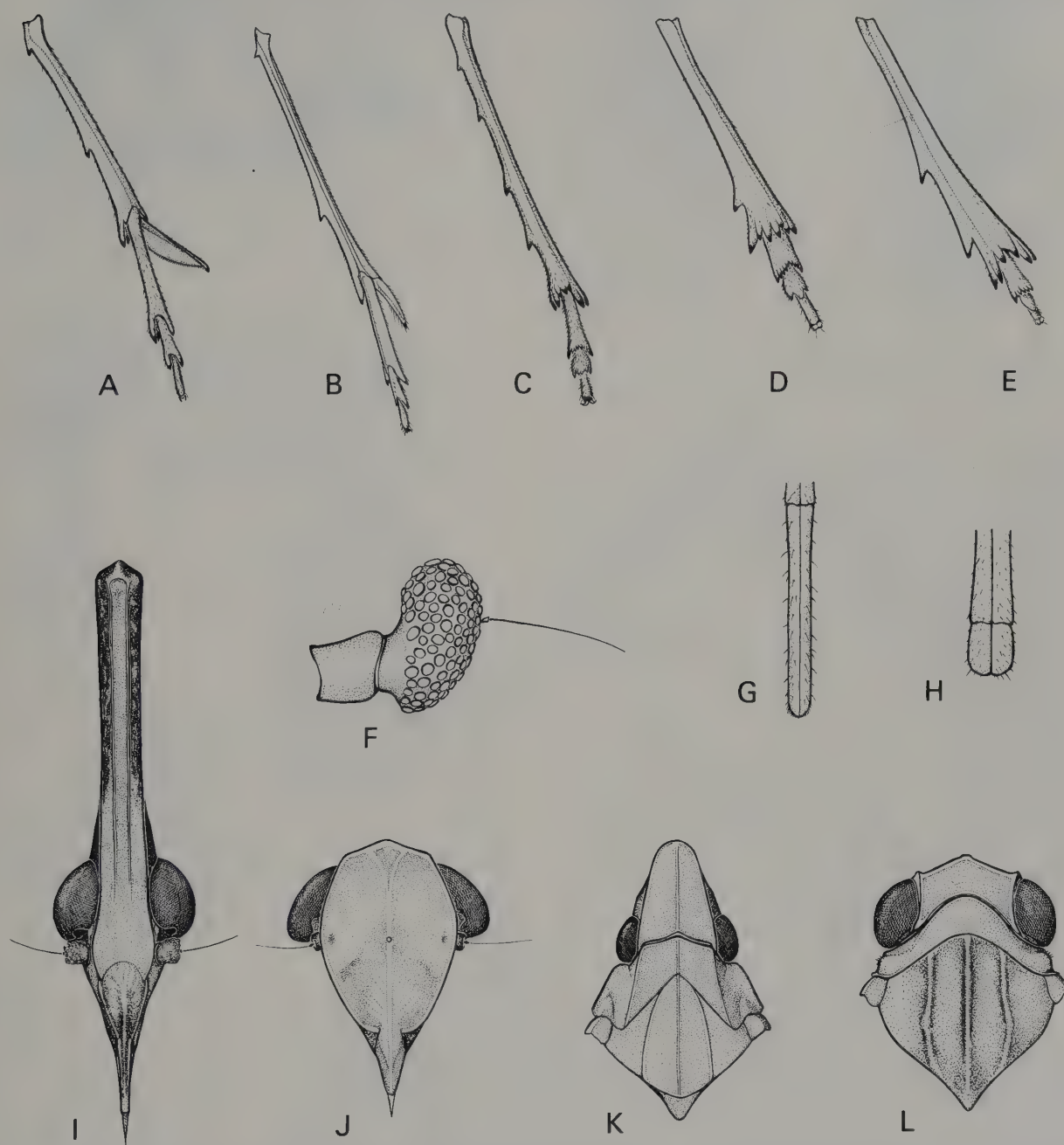


Fig. 30.37 Fulgoroidea: A, hind tibia and tarsus of *Perkinsiella saccharicida*, Delphacidae; B, same of *Ugyops* sp., Delphacidae; C, same, ventral, of *Desudaba psittacus*, Fulgoridae; D, same of *Massila sicca*, Flatidae; E, same of *Scolypopa australis*, Ricaniidae; F, antenna of *Desudaba psittacus*, Fulgoridae; G, apex of rostrum of *Desudaba psittacus*, Fulgoridae; H, same of *Zoraida* sp., Derbidae; I, facial view of head of *Thanatodictya praeferata*, Dictyopharidae; J, same of *Oliarus lubra*, Cixiidae; K, mesonotum of *Kallitambinia australis*, Tropiduchidae; L, same of *Salona panorpaepennis*, Nogodinidae. [S. Monteith]

32. Delphacidae (Araeopidae; Figs 30.37A, B, 38; 36.7B). Mostly small, from less than 2 to 9 mm in length to wing apex. A large movable spur at the apex of the hind tibia is diagnostic. Brachyptery and intra-specific alary dimorphism are common. Mostly feed on monocots. Nymphs are free roaming, like the adults. *Perkinsiella*

saccharicida, the sugarcane planthopper, a native of North Qld, and a vector of Fiji disease of sugar cane, was accidentally introduced into other cane-growing areas. The introduction into Hawaii of the mirid *Tythus mundulus*, a predator of eggs of *P. saccharicida*, is one of the outstanding successes in biological control (Clausen

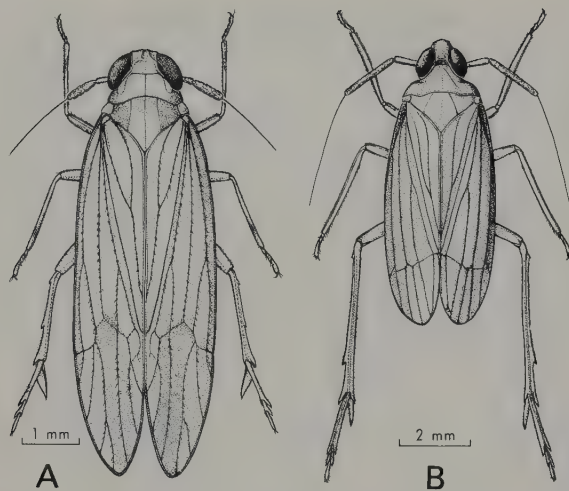


Fig. 30.38 Delphacidae: A, *Perkinsiella saccharicida*; B, *Ugyops* sp. [S. Monteith]

1978). The tropicopolitan *Peregrinus maidis* and *Sogatella kolophon* transmit viruses of grasses in Australia (Grylls 1979). In South-East Asia, *Nilaparvata lugens* is a vector of virus diseases of rice, but there is no evidence of their transmission in Australia.

More than 1500 species in 284 genera occur in the world. The Australian ASIRACINAE contain 13 species in three genera (Donaldson 1983b). The remaining 51 Australian species in 33 genera belong to DELPHACINAE. [Fennah 1965]

33. Cixiidae (Figs 30.37J, 39A). Cosmopolitan, with more than 1300 described species world-wide. The Australian species are contained in 15 genera, nearly half of them in *Oliarus*; many species remain undescribed. Cixiid nymphs are primarily root-feeders; some have been found in ant nests and some are subterranean cave dwellers with reduced eyes. Hacker (1925) described the life history of *Oliarus felis*, the nymphs of which live on grass roots and may be submerged by brackish water at high tide. [Fennah 1956]

34. Meenoplidae (Fig. 30.41D). Mostly rather small and inconspicuous and confined to the Eastern Hemisphere, with more than 100 described species. Australian species are contained in the NISIINAE, in *Phaconeura* (7 spp.), *Nisia* (2 spp.) and *Suva* (1 sp.), and all except *P. froggatti* and *P. caesa* from N.S.W. are restricted to tropical Australia. *P. pluto* from W.A. is cavernicolous, without eyes or ocelli, and is brachypterous, with weakly sclerotised integument (Fennah 1973). Meenoplid nymphs are root-feeders. [Muir 1925; Woodward 1957]

35. Fulgoridae (lantern flies; Plate 3, A; Figs 30.6A, 37C, F, G, 39B, C). Medium-sized to large species; most Australian species have a wing-span of 25–40 mm. Feed on trees and woody shrubs, feeding through bark. Eggs wax-covered. The world fauna comprises about 670, mostly tropical, species. Of the 8 Australian genera, *Desudaba* (7 spp.) is characterised by a brightly coloured patch at the base of the hind wing and a distinct callus on the vertex. Two species of *Birdantis* extend from New

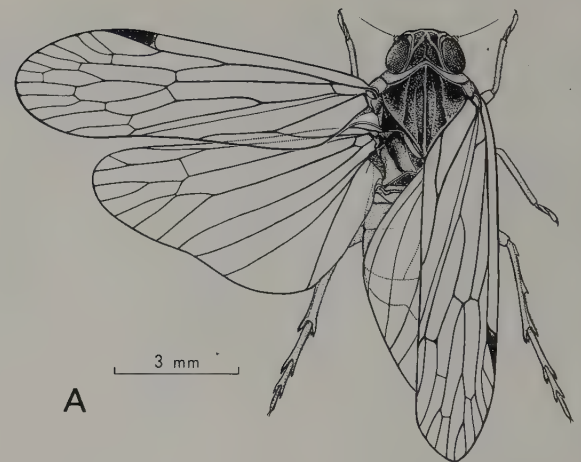


Fig. 30.39 A, *Oliarus lubra*, Cixiidae; B, *Eurinopsyche arborea*, Fulgoridae; C, facial view of head of *E. arborea*. [S. Monteith]

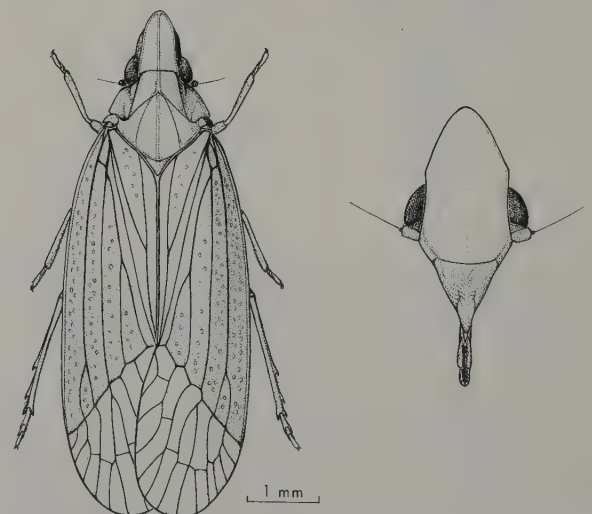


Fig. 30.40 *Kallitambinia australis*, Tropiduchidae, and facial view of head. [S. Monteith]

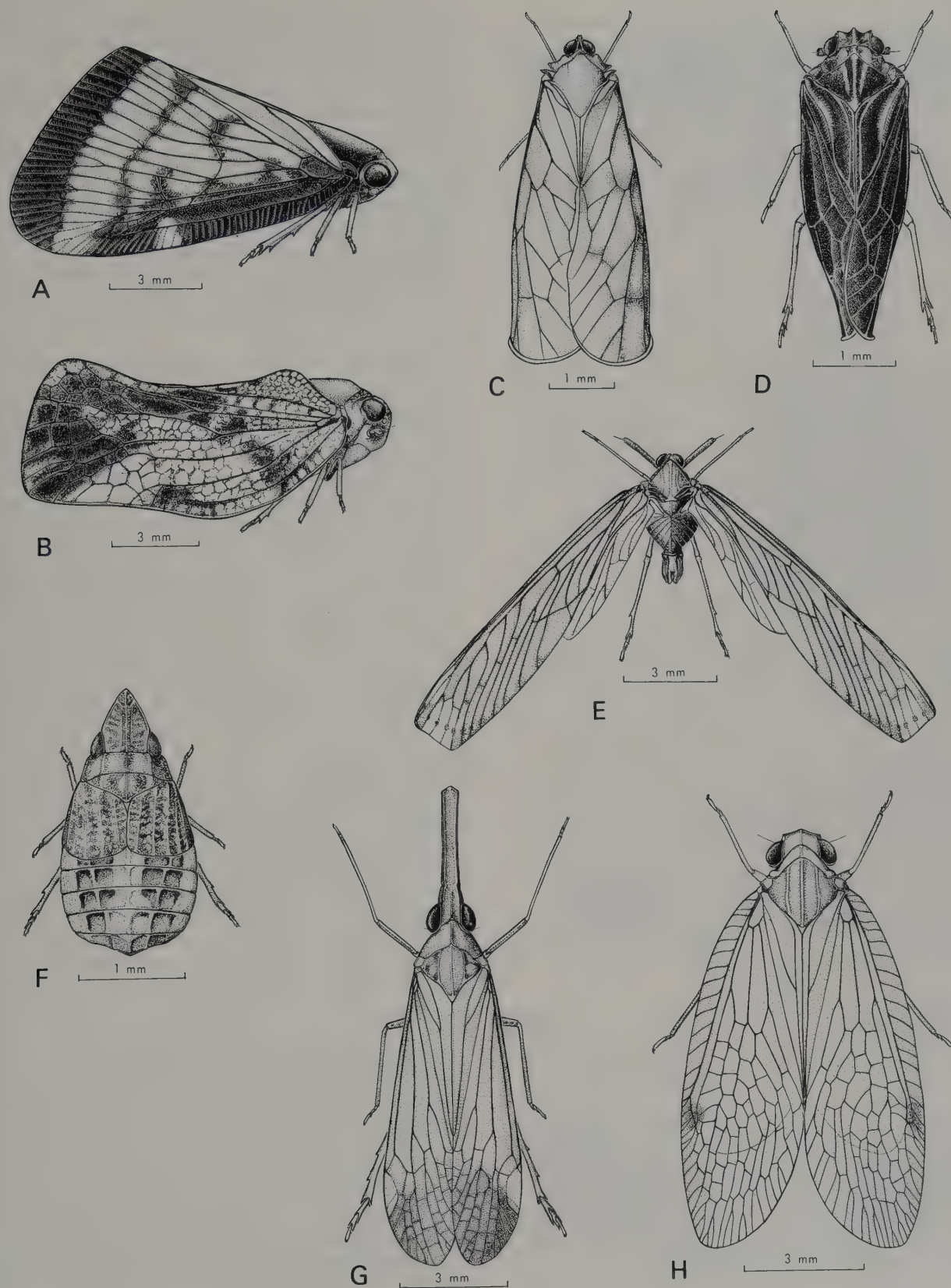
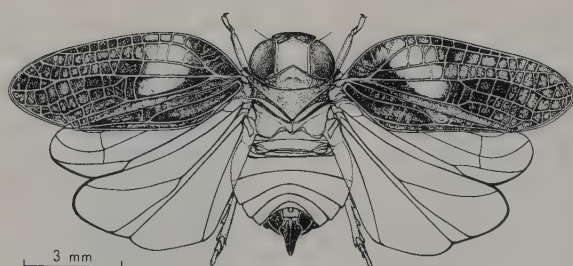
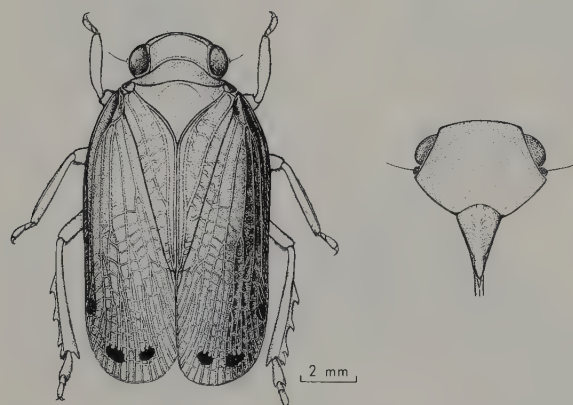


Fig. 30.41 A, *Scolypopa australis*, Ricaniidae; B, *Massila sicca*, Flatidae; C, unidentified sp. of Derbidae-Otiocerini; D, *Phaconeura froggatti*, Meenoplidae; E, *Zoraida* sp., Derbidae-Zoraidini; F, *Austrorgerius collinae*, Dictyopharidae; G, *Thanatodictya praeferrata*, Dictyopharidae; H, *Salona panorpaeppennis*, Nogodinidae. [S. Monteith]

Fig. 30.42 *Chlamydopteryx vulturnus*, Issidae.

[S. Monteith]

Fig. 30.43 A, *Platybrachys maculipennis*, Eurybrachyidae; B, facial view of head.

[S. Monteith]

Fig. 30.44 *Siphanta eberhardi*, Flatidae.

[A. E. Westcott]

Fig. 30.45 *Lophops saccharicida*, Lophopidae.

[S. Monteith]

Guinea to North Qld. The brown *Eurinopsyche obscurata* and *Rentinus dilatatus* have a long narrow snout projecting in front of the head. [Lallemand 1963]

36. Achilidae (Plate 3, B; Fig. 30.5A). Cosmopolitan, with about 380 described species; much of the Australian fauna is unnamed. Usually the fore wings are folded flat, partially overlapping at rest, although in some species they are tectiform. Clavus rather short, ending a little beyond half-way along the fore wing, and making a distinct angle with it. Most Australian species are brown to black, some are green; *Achilus flammeus* is bright red; *Aneipo* is usually brightly coloured (Lambkin 1978). Achilid nymphs live under bark or in cavities in dead wood; those of *A. flammeus* have also been found in termite nests. [Fennah 1950]

37. Derbidae (Figs 30.37H, 41C, E). Small to medium-sized, delicate species, often with striking patterns of yellow, brown or cream. Many adults feed on monocots; many nymphs live under bark and feed on fungi. Widespread in the tropics, with more than 800 species. *Rhotana chrysonoe*, with rather broad, yellowish wings, occurs in rainforest. *Zoraida* has a short body, but exceedingly long, narrow wings. [Fennah 1956; Zelazny 1981]

38. Dictyopharidae (Figs 30.37I, 41F, G). Medium-sized, usually with the head strongly prolonged anteriorly, and with rather narrow wings. Cosmopolitan, with more than 600 described species. The Australian fauna includes several species of *Thanatodictya*, which have brown markings on the fore wings, and *Hasta*, which are green. The nymph-like ORGERIINAE, all brachypterous and lacking tegulae, are widespread in arid and semi-arid regions; *Austrorgerius collinae* is the sole Australian representative (Woodward 1960).

39. Tropiduchidae (Figs 30.37K, 40). About 380 species, mostly tropical and subtropical. The wings of Tambiniini are mostly clear, with a distinct nodal line and cross-veins in fore wings restricted to the apical portion; the beautiful *Tambinia venusta*, from Qld, and the bright green *Kallitambinia australis*, common on mangroves in temperate Australia (M. J. Fletcher 1979b, 1981), are the only Australian representatives. *Trichoduchus biermani* with shiny dark-brown fore wings and subreticulate venation is the only Australian species of Trypetimorphini. The remaining Australian genera belong to Tropiduchini. [Fennah 1982]

40. Issidae (Fig. 30.42). Issids are mostly dull coloured, with unusual fore wings often shortened or convex and of roughened consistency. More than 1100 species are known, but the family is little known in Australia. *Chlamydopteryx* has convex, mottled, brown fore wings. *Gelastissus* (2 spp.) from Qld is brachypterous. [Fennah 1954]

41. Flatidae (Plate 3, C; Figs 30.37D, 41B, 44). Flatid fore wings are usually broad, triangular, steeply tectiform, opaque and brightly coloured, most commonly green. Nymphs usually sessile, producing copious wax filaments. Mainly tropicopolitan, with more than 1000 known species world-wide. *Siphanta* (40 spp.) is the largest Australian genus (M. J. Fletcher 1985). Myers (1922) has described the nymph of *S. acuta*, common on

Eucalyptus. Other common species are the greyish blue *Anzora unicolor* and the purple *Dworena hyacintha*. The costal and apical areas of the fore wing of *Mimophantia stictica* are deciduous, palisades of cells breaking off along a continuous line at CP (see Fig. 6.25) and the base of the apical cells. [M. J. Fletcher 1988]

42. Nogodinidae (Figs 30.37L, 41H). Mostly tropical and subtropical, with more than 130 species world-wide. Usually clear-winged, with many cross-veins. Though superficially resembling ricanjiids, they lack markings on the fore wings. Two common species are *Nurunderia chrysopoides* on *Eucalyptus* trunks in Qld and N.S.W., and *Salona panorpaepennis* in Qld. *Alleloplasis* (2 spp.) from arid areas of southern Australia, has elongate, strap-shaped, fore wings.

43. Eurybrachyidae (Plate 3, D, E; Figs 30.9D, 43). Mostly broad, squat, fairly large planthoppers, mottled with brown, red, yellow or orange coloration; some are black. They are predominantly Australian, Oriental, and Afrotropical, with over 170 species. The 10 genera and 46 species described from Australia belong in the Platybrachyini; Fennah (1964) provided a key to the genera. *Platybrachys* (17 spp.) is the largest genus. Some *Platybrachys* oviposit on the trunks of *Eucalyptus*, and their nymphs move further up the tree to feed (Hacker 1924). *Olonia* (9 spp.) and *Dardus* (6 spp.) are associated with *Acacia*.

44. Lophopidae (Fig. 30.45). More than 120 species are described world-wide. *Kasserota*, with transparent, elongate fore wings, contains the largest Australian species. *Lophops saccharicida* has yellowish brown fore wings with darker stripes and is found on sugar cane and other grasses in Qld.

45. Ricaniidae (Figs 30.37E, 41A). About 380 species are described world-wide. The temperate Australian *Scolypopa australis* is polyphagous and a pest of passion vines. The fore wings are hyaline and peripherally barred with dark brown (M. J. Fletcher 1979a). Adults and nymphs sit together in rows along stems. The abdomen of the nymph is upturned and bears apically a vertically disposed, fan-like corona of fine, waxy filaments. Honey produced by honey bees from the honeydew of *S. australis* feeding on *Coriaria arborea* in New Zealand is highly toxic to humans (Cumber 1966).

Suborder HETEROPTERA

The monophyly of the Heteroptera is established by several synapomorphies, some of which may be secondarily lost. They include: labium inserted well in front of prosternum with a sclerotised gular region intervening and allowing prognathous condition; reduced clypeal region; ocelli maximally 2; complex scent gland system developed, ventral in adult, dorsal in nymph; both pairs of wings lying flat over abdomen, the apical portions overlapping at rest; wing venation characteristically reduced; trachea of fused anal vein 'trapped' by CuA₂; CuP atrophied; claval furrow of hind wing usually bifurcate; wing coupling apparatus comprises setal/tuberculate 'clip' under fused anal vein of fore wing. Trichobothria present. Dorsal connexivum developed.

Alimentary filter system absent. Phytophagous species feed in parenchyma. Predacious and haematophagous, aquatic and semiaquatic groups occur.

Extensive accounts of the Heteroptera are given by Poisson (1951) and with special reference to the Australian fauna by Gross (1975a). N. C. E. Miller (1956) and Southwood and Leston (1959) have reviewed their biology. China and Miller (1959) have provided keys to subfamilies of adults, and DeCoursey (1971) and Herring and Ashlock (1971) keys to subfamilies of North American nymphs.

Infraorder COLEORRHYNCHA (PELORIDIOMORPHA, PELORIDIOPTERA)

by M. CARVER and G. F. GROSS

This small group contains only the Peloridiidae, and has a disjunct, circumantarctic distribution. Its relationships within the Hemiptera have been unclear, and its position has veered between the 'Homoptera' and Heteroptera since its first designation in 1897 (China 1962; Schlee 1969; J. W. Evans 1982; Hamilton 1981; Wootton and Betts 1986). Peloridiids are a tantalising mixture of primitive and specialised, 'homopteran' and heteropteran features. Ancestral features include a complete tentorium, discrete pro- and mesothoracic ganglia and a full complement (8 pairs) of abdominal spiracles. The disposition and venation of both the fore and hind wings and the wing coupling apparatus are heteropteran, as are the presence of a gula, keeled propleura, trichobothria, cryptocerate antennae and mycoid microsculpture. The family has therefore been returned to the Heteroptera as a sister group of the rest of the Heteroptera (Fig. 30.14).

The sister-group of the Coleorrhyncha, namely the rest of the Heteroptera, is characterised by the presence of nymphal dorsal scent glands variously and intersegmentally on T3–T7; and by a reduced tentorium.

Superfamily PELORIDIOIDEA

46. Peloridiidae (Fig. 6.25r; 30.46). Of the 25 species in 12 genera, 5 species in 4 genera (*Hemiodoecus*, *Hemiodoecellus*, *Hackeriella*, *Hemiwoodwardia*) have

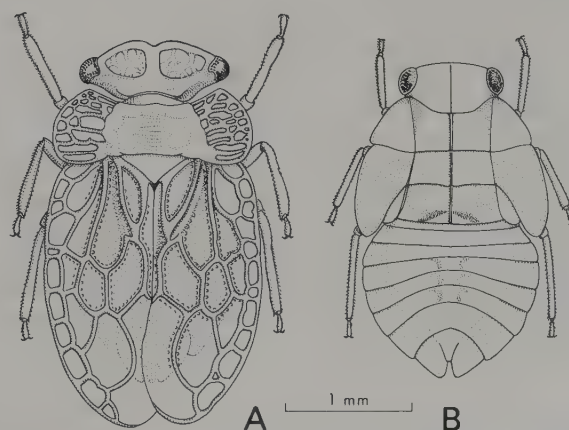


Fig. 30.46 *Hemiodoecellus fidelis*, Peloridiidae; A, adult; B, final instar nymph. [F. Evans]



Fig. 30.47 *Oncyclocotis* sp., Enicocephalidae, and fore tibia and tarsus enlarged. [S. Monteith]

been recorded from eastern Australia and Tas. *Howeria* (3 spp.) is known from Lord Howe I., and *Oiophysella* (1 sp.) from New Caledonia. The remainder occur in New Zealand and southern South America.

Most commonly occur cryptically among wet moss and hepatics in cool rainforests, often associated with *Nothofagus*, or, sometimes, in alpine sphagnum bogs. Dry periods may be spent among leaf litter.

Adults small (2–5 mm), flat, greenish brown, slow moving, often enveloped in a thin, skin-like film. Head produced anteriorly and interocularly to form thin expansion, which usually bears 2 hyaline areolae; very transverse, with prominent lateral eyes; opisthognathous but with gula. Antennae small, 3-segmented, ventrally situated. Rostrum flanked by propleural keels. Pronotum large, with extensive lateral paranota which may have a few large, hyaline areolae or numerous smaller ones or these may be absent. All known species except *Peloridium hammoniorum* from South America are flightless and sub-macropterous, and without hind wings and ocelli. *P. hammoniorum* is dimorphic, with both macropterous and sub-macropterous adults. Macropters also possess hind wings, a wing-coupling apparatus and 2 ocelli, and can fly. The fore wings lie flat over the abdomen, the apical portions considerably overlapping in the macropter. Hyaline areolae lie between the hyaline veins, and the expanded costal region is cross-veined. The hyaline patterning perhaps provides camouflage in their watery

environment. The New Caledonian species lacks areolae and veins. Internally, an alimentary filter system is absent, but mycetomes are present.

Nymphs of some instars of some species have both dorsal and ventral sutures separating the developing mesothoracic wing pads and paranota from the rest of the thorax. These and the nature of the paranotal tracheation suggested to earlier authors that the pronotal paranota are homologous with wings. They are more likely however to be specialised expansions like those of the head and costal area of the fore wing. [China 1962; Evans 1982]

Infraorder ENICOCEPHALOMORPHA

by G. F. GROSS, P. ŠTYS and M. CARVER

The Enicocephalomorpha are a basal group of Heteroptera (Schuh 1981; Štys 1981, 1989). Head transversely bilobed, ocelli on posterior lobe. Fore legs uniquely raptorial. Proximal cross-vein in fore wing retained; pilose ambient (peripheral) vein and costal fracture present; RP branched (in one non-Australian genus). Ventral scent gland of adult opens medially near abdomen; dorsal scent gland of nymph opens medially on T4 and remains functional in adult. Paired auchenorrhyncha-like genital plates in some taxa; unique modifications of both male and female genitalia including, in male, either absence of a true phallus, or the intromittent organ external and permanently everted.

The sister-group of the Enicocephalomorpha (Dipso-coromorpha + Gerromorpha + Leptopodomorpha + Nepomorpha + Cimicomorpha + Pentatomomorpha) is the Euheteroptera of some authors (Schuh 1986a; Štys 1985a) (Fig. 30.14). It is characterised by synapomorphies mostly of a reductional nature, including loss of proximal cross-vein in fore wing and reduction of ambient vein, especially postero-apically; and migration of ventral scent gland openings anteriorly to thorax. Male pygophore capsular, enclosing an erectile, basally anchored phallus; parameres attached to pygophore either externally or internally.

Superfamily ENICOCEPHALOIDEA

Small to medium sized bugs (1.0–17 mm), superficially resembling reduviids; probably generalised predators of other small arthropods in leaf litter, rotting logs, tussocks or under stones. Macropters sometimes seen in swarms at dusk, and may be attracted to light in large numbers. Many species exhibit alary polymorphism or dimorphism, some are inherently brachypterous or apterous, or have flightless females. Tarsal formula of nymphs 1:1:1; of adults, 1:2:2, rarely 1:1:1 or 2:2:2. The eggs have a thin, simple permeable chorion and perhaps hatch only under humid conditions. Mostly tropical and subtropical but in the Southern Hemisphere extend to some of the sub-antarctic islands (e.g. Crozet Is, living in penguin and albatross nests).

Key to the Families of Enicocephaloidea Known in Australia

- Pronotum divided by two transverse sulci into three distinct, laterally constricted areas (Fig. 30.47) **Enicocephalidae**
 Pronotum not divided by two transverse sulci into three distinct, laterally constricted areas **Aenictopecheidae**

47. Aenictopecheidae have a costal fracture in fore wing, external intromittent male organ, and most retain an ovipositor. Distribution is Gondwanan, with a single Holarctic genus. Four subfamilies recognised. *Australostolus monteithi* (AENICTOPECHEINAE) from N.S.W. and S.A., and *Nymphocoris hilli* (NYMPHOCORINAE) from Tas. are the only Australian species. [Štys 1988]

48. Enicocephalidae (Figs 30.5B, 47) have a cosmopolitan distribution. Male genitalia reduced to a racquet-shaped guide attached to the pygophore. Five subfamilies recognised. Australian species belong to *Systelloderes*, *Henschiella*, *Oncyclocotis* and *Usingeriella* in ENICOCEPHALINAE; many, especially of *Oncyclocotis*, are undescribed. *O. tasmanicus* has been studied by Hickman and Hickman (1981). The apterous Monteitholini (Phthiocrininae) with paired auchenorhyncha-like genital plates are known only from New Caledonia but may occur in Australia as could also the Phallopiratinae, an Oriental group. [Štys 1978, 1981]

Infraorder DIPSOCOROMORPHA

by L. HILL, G. F. GROSS and M. CARVER

Another basal group of the Heteroptera. Possess plesiomorphic features in the digestive and scent gland systems, wing structure and wing venation. Synapomorphies include articulated, paramere-like laterotergites on pre-

genital segments of male; frequently asymmetrical male genitalia; articulation of parameres with basal plate; sexual dimorphism in tarsal formula; characteristic spermathecal pump; often a pair of spiculate (adhesive?) pads medially on hind coxae. Excluding the Stemmocryptidae, the Dipsocoromorpha are most easily recognisable by the short scape and pedicel and long, slender, long-haired, 2-segmented flagellum of the antenna. All members are small (less than 3 mm) and probably predacious. The eggs of Dipsocoridae are unlike those of any other Heteroptera (Cobben 1968).

The sister-group of the Dipsocoromorpha, the Neo-heteroptera (Schuh 1986a), comprises Gerromorpha + Leptopodomorpha + Nepomorpha + Cimicomorpha + Pentatomomorpha (Fig. 30.14), and is characterised by loss of peripheral venation and fused anal vein in fore wing, symmetry of abdominal segmentation and absence of dipsocoromorphan autapomorphies, especially in the male genitalia.

Superfamily DIPSOCOROIDEA

Three of the five families recognised occur in Australia; Stemmocryptidae, described from New Guinea (Štys 1983), may yet be found in North Qld. Hysipterygidae are restricted to Africa. The biology of Dipsocoroidea has been little studied; all species probably require humid conditions. [Štys 1970; Emsley 1969]

Key to the Families of Dipsocoroidea Known in Australia

1. First two antennal segments (scape and pedicel) subequal; labium 3–4-segmented, costal fracture usually only marginal **Schizopteridae**
- Pedicel of antenna twice as long as scape (Figs 30.48A, B); labium 4-segmented 2
- 2(1). Costal fracture reaching centre of fore wings (usually macropterous, sometimes brachypterous) (Fig. 30.48B); labium reaching only to fore coxae **Dipsocoridae**
- Costal fracture marginal (macropterous to micropterous and coleopteroid) (Fig. 30.48A); labium usually reaching hind coxae **Ceratocombidae**

49. Ceratocombidae (Fig. 30.48A). Two subfamilies and seven genera world-wide (Štys 1982, 1983). Macropterous or brachypterous; 2 non-Australian genera coleopteroid. Only the primitive, cosmopolitan *Ceratocombus* occurs in Australia, with one described and several undescribed species. They are small (2 mm), brown or yellowish brown, swiftly running species, with well-developed ovipositors. *C. australiensis* occurs widely in a variety of moist habitats (L. Hill 1980).

50. Dipsocoridae (Fig. 30.48B). This family contains only two genera; represented in Australia by 4 described and many undescribed species of *Cryptostemma* (L. Hill 1987a). Small (2–3 mm), brown with a grey fore wing sheen. They live interstitially in gravel on river banks at all altitudes and run rapidly; macropters are common and fly readily. Male abdomen and genitalia asymmetrical; females with short membranous ovipositor.

51. Schizopteridae (Fig. 30.48C). This, the largest dipsocoroid family has 41 genera; 12 genera with 38 species have been described from Australia but many undescribed

species are known, especially from wet, eastern forests. Habitats include leaf litter, logs, bogs and ant nests. Mostly small (1–3 mm) compact (or rotund) species. Head usually declivous. Have a characteristic slow unsteady gait and can hop several centimetres. Pits, depressions or glands of unknown function common in male. Coleopterism common in female. Three subfamilies recognised, all of which are represented in Australia. HYPSELOSOMATINAE are most primitive and have very large eyes, 4-segmented labium and well-developed ovipositor (L. Hill 1984, 1987b). *Macromannus webbicus* is only 1 mm long. OGERIINAE have normal-sized eyes, 4-segmented labium and reduced ovipositor. *Pachyplagia australia* is an inquiline with ponerine ants. *Ogeria* sp. frequents hollow logs and may also be an inquiline. SCHIZOPTERINAE have normal-sized eyes, 3-segmented labium and reduced ovipositor. They include *Pachyplagioides* and *Pinochius*. *Dictyonannus*, as yet unplaced in a subfamily, is convex with a porrect head. [Emsley 1969]

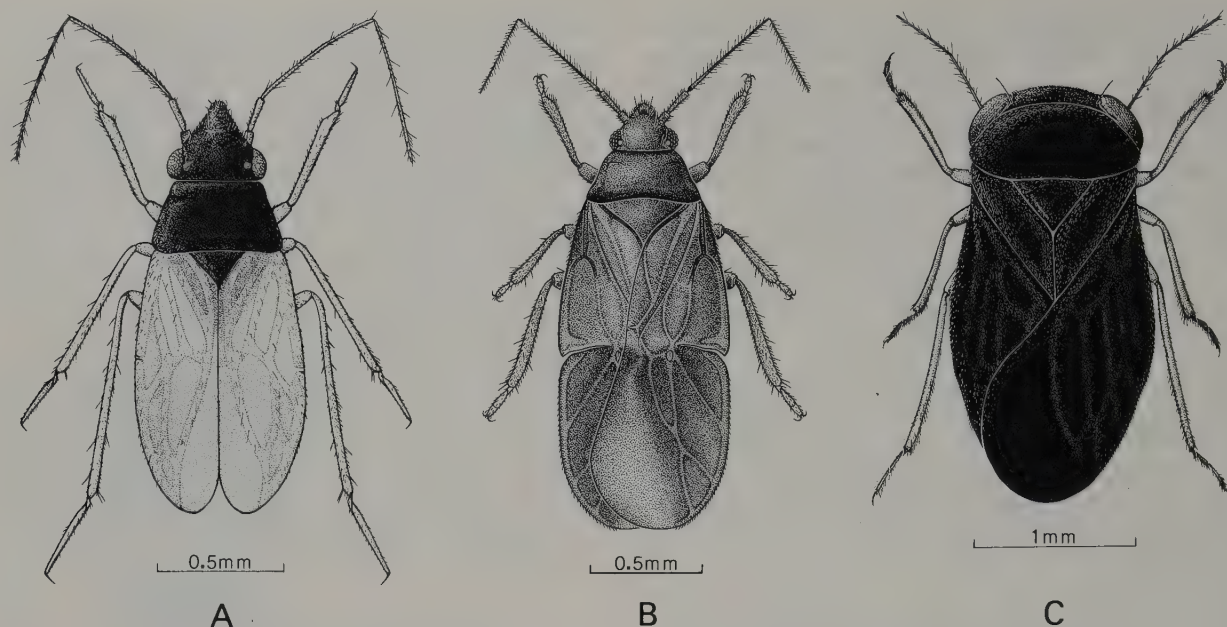


Fig. 30.48 A, *Ceratocombus australiensis*, Ceratocombidae; B, *Cryptostemma monga*, Dipsocoridae; C, undescribed genus of Schizopteridae.

[A, C by S. Monteith; B by S. P. Kim]

Infraorder GERROMORPHA (AMPHIBICORISAE, AMPHIBICORIOMORPHA)

by G. F. GROSS, I. LANSBURY, J. T. POLHEMUS and T. A. WEIR

N. M. Andersen (1982) concluded that the Gerromorpha are monophyletic and retain many features of the heteropterous ground plan, especially in the structure of the egg, head and male phallus. Possible synapomorphies for the group are the type and distribution of cephalic trichobothria, quadrangular mandibular levers, dorsal and ventral pretarsal arolia, reduced clavus, and the structure of the female genital tract. Gerromorpha include most, but not all, families of semiaquatic bugs and are the most diverse group of animals associated with water surfaces. Gerromorphs are polyphagous predators or scavengers, mostly of other arthropods. There are two basic types of predators: searching, and rather solitary, predators such as *Mesovelina* (Mesoveliidae), *Hebrus* (Hebridae) and *Hydrometra* (Hydrometridae), and waiting predators, often forming dense aggregations, such as most gerrids and veliids. Alary polymorphism is very common and wing autotomy is also known.

The sister group of the Gerromorpha is the Panheteroptera (Leptopodomorpha + Nepomorpha + Cimicomorpha + Pentatomomorpha) (Fig. 30.14) which is characterised by a heterogeneous (heteropterous) wing, i.e. with a coriaceous base (corium and clavus) providing support and protection, and a deformable, membranous apex for purposes of flight.

Superfamily MESOVELIOIDEA

52. Mesoveliidae (Fig. 30.49c). Mesoveliids are long-legged, slender predators. *Mesovelina* is cosmopolitan. *M. vittigera* and *M. hungerfordi* are common and associated with the surfaces and edges of fresh, standing waters,

especially those overhung by vegetation or having floating water plants. They also occur on brackish estuarine waters. There are both winged and wingless morphs, and the membranes are often torn from the hemelytra of winged forms, possibly to assist in mating. *Austrovelia queenslandica* is a wingless species which lives in leaf litter at high altitudes in North Qld and is related to similar terrestrial forms from New Guinea, New Caledonia and New Zealand (Malipatil and Monteith 1983). MESOVELIINAE are cosmopolitan but Madeoveliinae occur only in the Neotropics and Africa. [N. M. Andersen and Polhemus 1980; N. M. Andersen 1982]

Superfamily HEBROIDEA

53. Hebridae (Fig. 30.49b). Only 2 genera of HEBRINAE occur in Australia. *Hebrus axillaris* is a small, stout, velvety bug, 1–2 mm long, found in marginal vegetation by fresh water. Several other *Hebrus* species occur in litter in Qld rainforests. *Merragata hackeri* is of similar size and is quite common on stagnant pools in Vic., N.S.W., Qld and the N.T. The subfamily Hyrcaninae includes only 4 Oriental species. [N. M. Andersen 1981, 1982]

Superfamily HYDROMETROIDEA

Of the three included families only the Hydrometridae occur in Australia. Macroveliidae are found only in the Americas and the Paraphrynoveliidae only in southern Africa.

54. Hydrometridae (Fig. 30.49a). Of the three recognised subfamilies only HYDROMETRINAE occur in Australia and all species belong to the cosmopolitan *Hydrometra*. These small, slender water striders or marsh treaders are distinguished by their long head with the eyes placed near the middle. They are slow-moving predators

which occur along the vegetated margins of rivers and streams where the current is subdued, and along the edges of lakes, ponds and pools. Alary dimorphism occurs with apterous and micropterous forms predominating. *H. ris-*

beci and *H. strigosa* are widely distributed, with the former occurring also on New Caledonia, Norfolk I. and in New Zealand. The other Australian species are restricted to northern areas. [N. M. Andersen 1977, 1982]

Superfamily GERROIDEA

Key to the Families of Gerroidea Known in Australia

1. Head strongly deflected anteriorly and at least three times as long as wide; claws of mid and hind legs inserted apically on last tarsal segment; abdominal scent gland orifice present on T4; apterous **Hermatobatidae**
 Head correct, no more than twice as wide as long; claws of all legs inserted preapically on last tarsal segment; abdominal scent gland orifice absent; apterous or macropterous 2
- 2(1). Legs extremely long and slender (Fig. 30.51); hind femora usually more slender than mid femora, extending beyond apex of abdomen; fore coxae widely separated from mid coxae; fore tibia of ♂ without grasping comb; head without a medial, impressed line on dorsal surface; medial margins of eyes usually sinuate **Gerridae**
 Legs usually shorter (Fig. 30.50); hind femora usually stouter than mid femora, extending beyond apex of abdomen or not; fore coxae much closer to mid coxae or mid coxae equidistant between fore and hind coxae; fore tibia of ♂ with a grasping comb of short spines along inner margin; head with a distinct, impressed line on dorsal surface; medial margins of eyes straight or faintly curved **Veliidae**

55. Hermatobatidae. These wingless bugs with broad, distinctly flattened bodies are rarely collected though probably quite common. They are exclusively marine, being found in the lowest part of the intertidal zone of coral atolls and reefs, and oceanic islands of volcanic origin in the tropics. Species of *Hermatobates* skate very quickly on the surface at low tide, and seek pockets of air in the coral or rock as the tide comes in. Several species, including *H. haddoni* (Polhemus 1982), occur around the northern coast. [N. M. Andersen and Polhemus 1976; Cheng 1977; N. M. Andersen 1982]

56. Veliidae (Fig. 30.50). Three of the 6 subfamilies

occur in Australia. All live on the surface of water. RHAGOVELIINAE are represented by one species of the nearly cosmopolitan *Rhagovelia*, *R. australica*. MICROVELIINAE are represented by the cosmopolitan genus *Microvelia* (about 25 spp.; Malipatil 1980) which comprises small (about 1.4–3.7 mm long), dark bugs. Most live in quiet, nearshore freshwater areas with emergent vegetation and floating leaves. Some form large aggregations. Alary dimorphism is common with some species having both macropterous and apterous forms and other species having only one or other form. HALOVELIINAE are represented by *Halovelia* (4 spp.), *Xenobates*

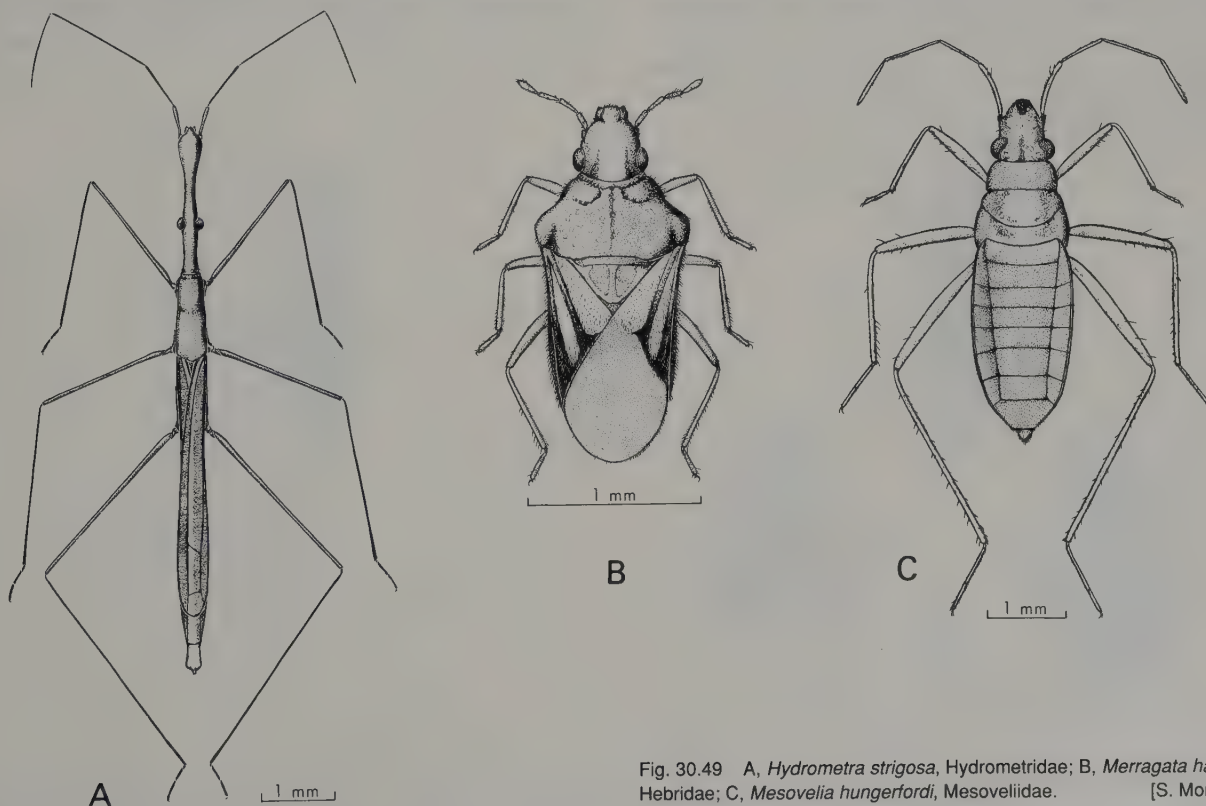


Fig. 30.49 A, *Hydrometra strigosa*, Hydrometridae; B, *Merragata hackeri*, Hebridae; C, *Mesovelia hungerfordi*, Mesoveliidae. [S. Monteith]

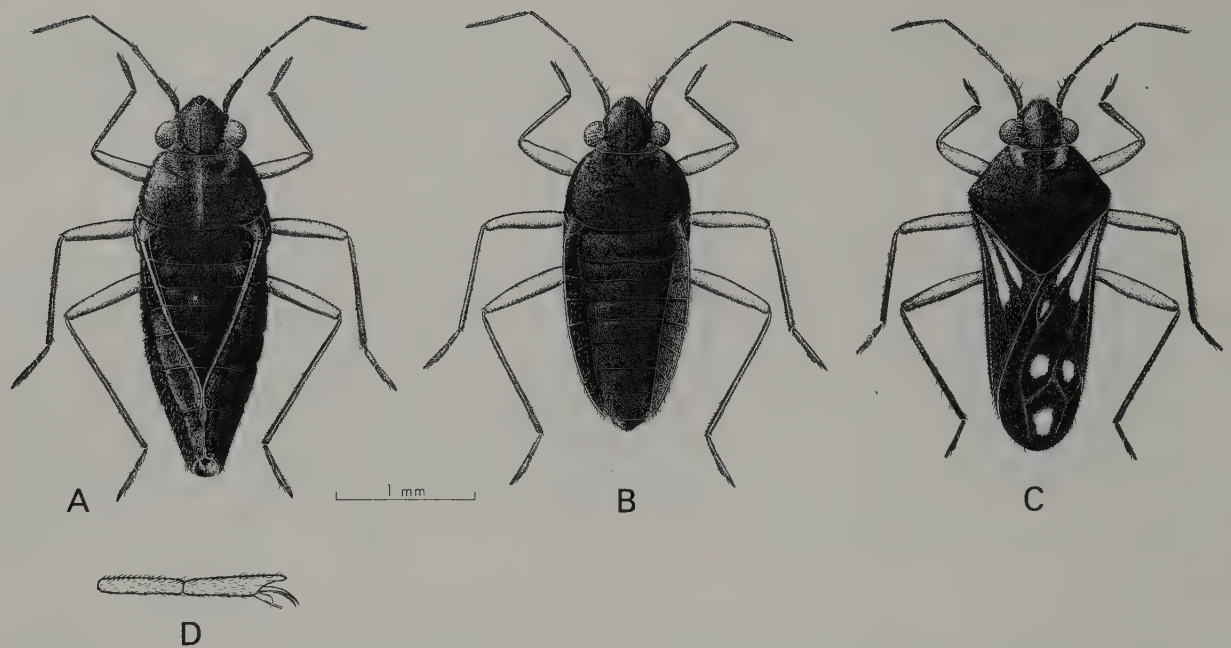


Fig. 30.50 *Microvelia peramoena*, Veliidae: A, ♀, apterous; B, ♂, apterous; C, ♂, macropterous; D, hind tarsus (enlarged).

[S. Monteith]

(about 7 spp.) and *Colpovelia* (2 spp.) which inhabit marine, intertidal zones in northern Australia (Polhemus 1982). [N. M. Andersen 1982]

57. Gerridae (Figs 3.10; 30.51). These are the true 'water striders' and include small to large species which are mostly long legged and skate rapidly on the surface of the water. Some tropical species are shared with southern New Guinea. Of the 8 subfamilies, 4 occur in Australia. The RHAGADOTARSINAE, the only gerrids in which females possess an ovipositor, are represented by *Rhagadotarsus*

(1 sp.) in northern Australia. Rhagadotarsinae are found in lakes, temporary pools or the quiet parts of flowing waters, usually in large aggregations. Communication during mating involves signals formed by patterned sequences of surface waves produced by leg movements (Wilcox 1972). TREPOBATINAE are represented by the broadly ovate *Rheumatometra* (2 spp.) which forms large aggregations in streams; in northern Australia by about 3 undescribed, freshwater species of another genus; and by the marine *Stenobates* (1 sp.). GERRINAE are mostly large

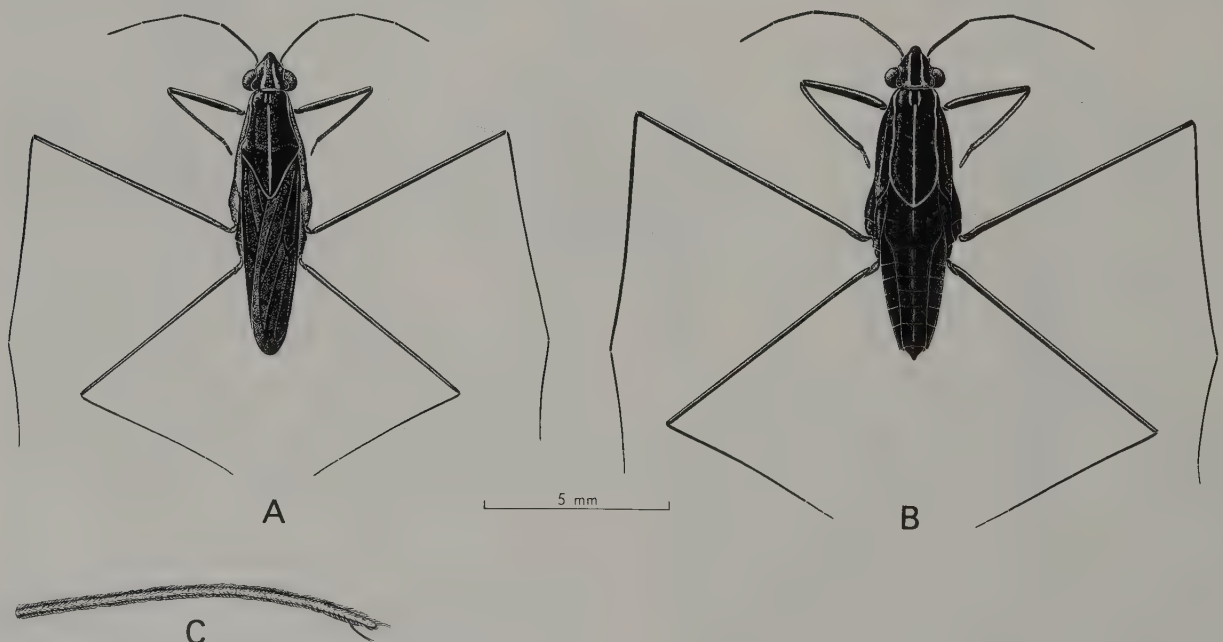


Fig. 30.51 *Limnogonus luctuosus*, Gerridae: A, macropterous; B, apterous; C, hind tarsus (enlarged).

[S. Monteith]

and commonly show wing dimorphism. *Aquarius*, *Limnogonus* (4 spp.), *Tenagonus* (4 spp.) and the endemic *Tenagogeris* (2 spp.) occur in Australia. HALOBATINAE are represented around northern coasts from Shark Bay (W.A.) to Sydney (N.S.W.) by 13 species

of the widespread and almost exclusively marine genus *Halobates*. Some of the species are always found close to the coast, others roam the tropical oceans (Malipatil 1988). [Hungerford and Matsuda 1960; Matsuda 1960; Calabrese 1980; N. M. Andersen 1982]

Infraorder LEPTOPODOMORPHA

by G. F. GROSS, J. T. POLHEMUS, I. LANSBURY and T. A. WEIR

Members of this group are all predacious and generally semiaquatic, perhaps in some cases fully aquatic. Leptopodomorphs have adopted a side by side copulatory position with a unique complementary modification of the

male abdomen to grasp the female fore wing. Schuh *et al.* (1987) have published a world catalogue and bibliography of the group.

Superfamily LEPTOPODOIDEA

Key to the Families of Leptopodoidea Known in Australia

- Beetle-like; hemelytra without membranes and meeting in a straight line; labium long, reaching or surpassing mid coxae; labium and fore femora without long spines; ocelli not situated on a tubercle; eyes prominent but not pedunculate; less than 2 mm long (Fig. 30.53c); one intertidal species on the Great Barrier Reef **Omaniidae**
- Not beetle-like; hemelytra with overlapping membranes; labium short, not passing prosternum; 1st and often 2nd segment of labium and fore femora with very long spines; ocelli set close together on a median tubercle; eyes set on short, broad peduncles; more than 2 mm long (Fig. 30.52) **Leptopodidae**

58. Leptopodidae (Fig. 30.52). These slender bugs frequent the drier parts of rock walls and boulders, usually near or in streams. *Valleriola* occurs in coastal Qld and the N.T. on rocks bordering fast-flowing streams. The Asian genus *Leotichius* seeks very dry, sheltered habitats such as shallow caves. [Polhemus and Polhemus 1987]

59. Omaniidae (Fig. 30.53c). Omaniids are small, beetle-like, flightless bugs distributed widely from the Pacific Ocean to Arabia. *Corallocoris marksae* is known from the Great Barrier Reef as well as New Caledonia, Samoa, Kwajalein and Singapore. During high tides

adults and nymphs retreat into fine crevices and channels in coral blocks. [Woodward 1958]

Superfamily SALDOIDEA

This group now includes only the Saldidae, and the intertidal Aepophilidae which are found only on the Atlantic coast of Europe and North Africa (Schuh and Polhemus 1980).

60. Saldidae (shore bugs; Figs 30.53A, B). Saldids are elongate or oval bugs usually mottled with light and dark to match their substrate. Their habitats are always marginal to fresh or salt water, including stream boulders or waterfall splash zones, damp fields and boggy areas. Australian species belong to *Pentacora* (CHILOXANTHINAE), *Saldula*, *Saldoida* and *Salduncula* (SALDINAE). [Cobben 1980; Polhemus 1985]

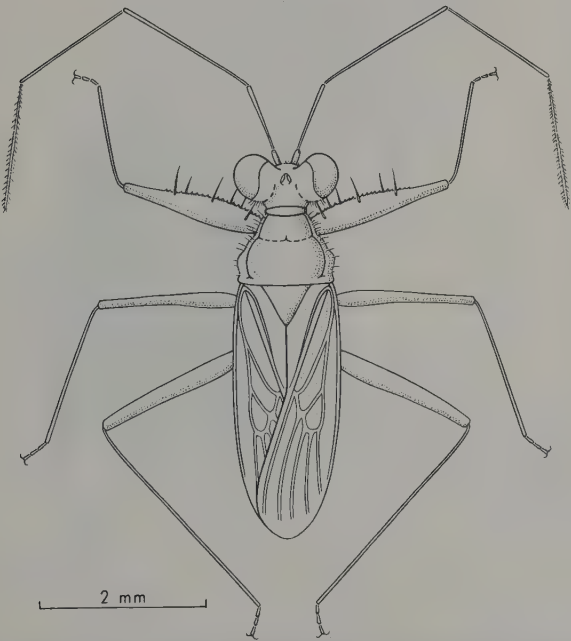


Fig. 30.52 *Valleriola wilsoni*, Leptopodidae.

[T. Nolan]

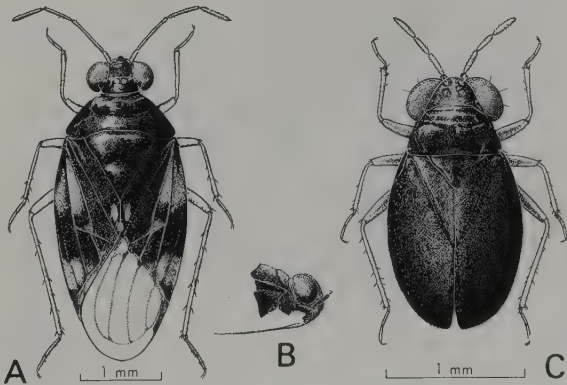


Fig. 30.53 A, *Saldula brevicornis*, Saldidae; B, lateral aspect of head of same; C, *Corallocoris marksae*, Omaniidae.

[S. Monteith]

Infraorder NEPOMORPHA (HYDROCORISAE, CRYPTOCERATA)

by G. F. GROSS, I. LANSBURY, J. T. POLHEMUS and T. A. WEIR

In this group of mostly predacious bugs the antennae are not visible from above or only the apical parts can be seen as in the Ochteroidea and *Aphelocheirus* (Naucoridae). The ochteroids are mostly riparian, whereas the

other nepomorphs are truly aquatic, subsurface dwellers with a diversity of methods for breathing while underwater. Some have raptorial fore legs to feed on large prey such as tadpoles and small fish.

Superfamily NEPOIDEA

Key to the Families of Nepoidea Known in Australia

- Apex of abdomen with a respiratory siphon composed of 2 angular filaments; siphon either short or as long as body (Figs 30.54A, B)..... **Nepidae**
 Apex of abdomen without a respiratory siphon but with 2 short, flat and retractable respiratory filaments (Figs 30.55A, B)..... **Belostomatidae**

61. Nepidae (Figs 30.54A, B). Underwater respiration is usually by means of a respiratory siphon that is pushed up through the surface film. The NEPINAE (water scorpions) are represented by *Laccotrephes tristis* which occurs in all

mainland states, and several undescribed species. The more slender RANATRINAE are represented by species of *Ranatra*, *Austronepa*, *Goondnomdanepa* and *Cercotmetus*. *Goondnomdanepa* is found under rocks in flowing

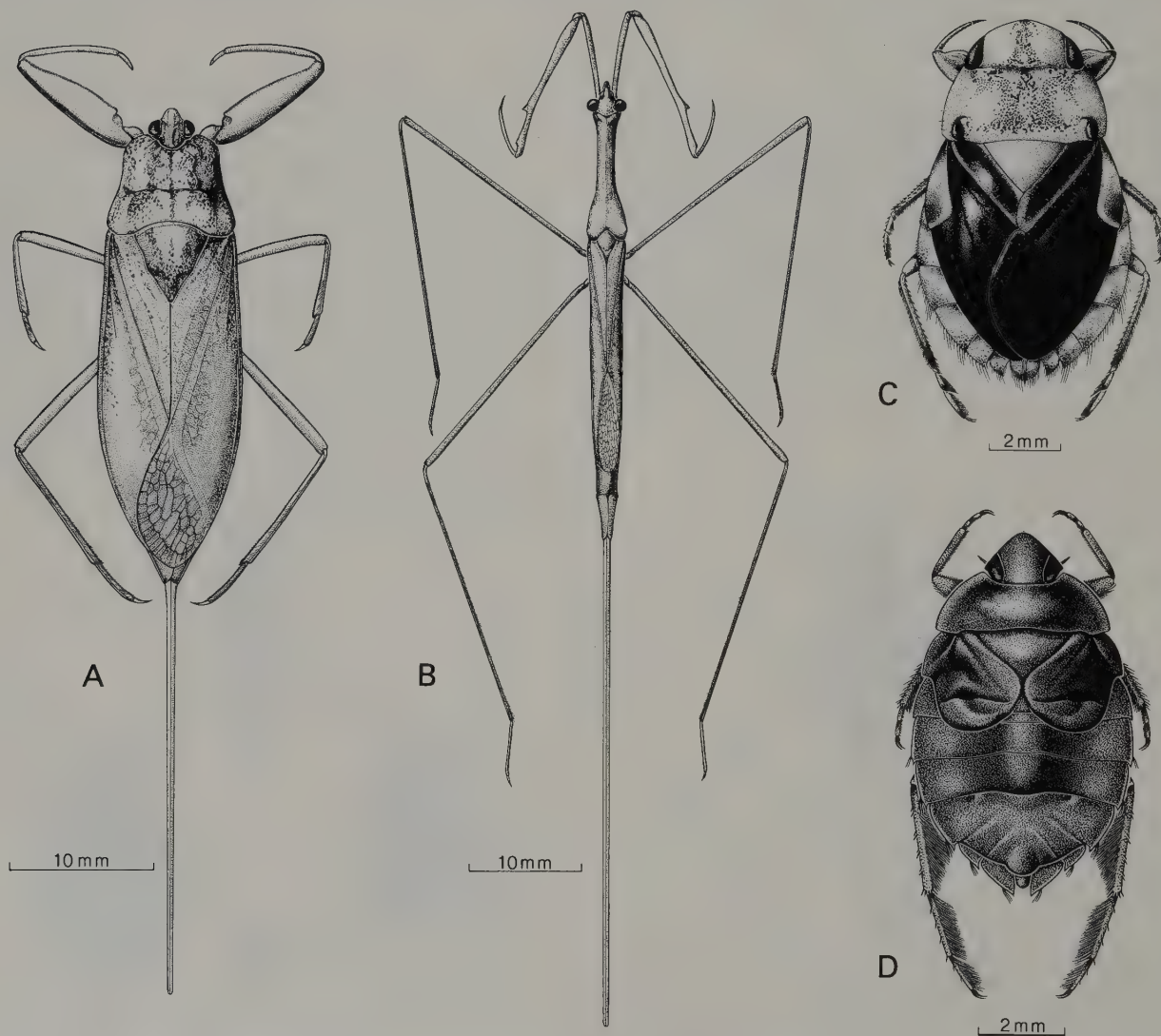


Fig. 30.54 A, *Laccotrephes tristis*, Nepidae; B, *Ranatra dispar*, Nepidae; C, *Naucoris congrex*, Naucoridae; D, *Aphelocheirus australicus*, Naucoridae.

[A, B by S. Monteith; C by T. Nolan; D by S. P. Kim]

water. All other nepids spend most of their time among water-weeds and in mud in ponds, lakes and streams. [Lansbury 1972, 1974, 1975a, 1978a]

62. Belostomatidae (Figs 3.7C; 30.55). The giant waterbugs belong to the LETHOCERINAE. The Australian species of *Lethocerus*, *L. insulanus* and *L. distinctifemur*,

with 50–70 mm long adults, are the largest Australian Heteroptera, and sometimes a nuisance in fish farms. The smaller and more oval BELOSTOMATINAE are represented by *Diplonychus* (= *Sphaerodema*) *rusticus* and *D. eques*; their females oviposit on the dorsum of the males which care for the eggs. [Menke 1960]

Superfamily OCHTEROIDEA (GELASTOCOROIDEA)

This group is best represented in the Australian region and the New World.

Key to the Families of Ochteroidea Known in Australia

Fore legs not raptorial, similar in form to other legs (Fig. 30.56A); labium long, reaching to at least hind coxae; apical part of antennae usually visible from above; scutellum somewhat convex and finely punctate **Ochteridae**
Fore legs raptorial with broadened femur (Fig. 30.56B); labium short, not reaching behind fore coxae; antennae not visible from above, held in grooves beneath eyes; scutellum with low keels or swellings and rugulose **Gelastocoridae**

63. Ochteridae (Fig. 30.56A). All species are littoral predators, especially in sandy stretches around the margins of slightly saline lakes. The nymphs occur either just under the surface of shallow water or partially buried in sand; grains of sand frequently adhere to their dorsal sur-

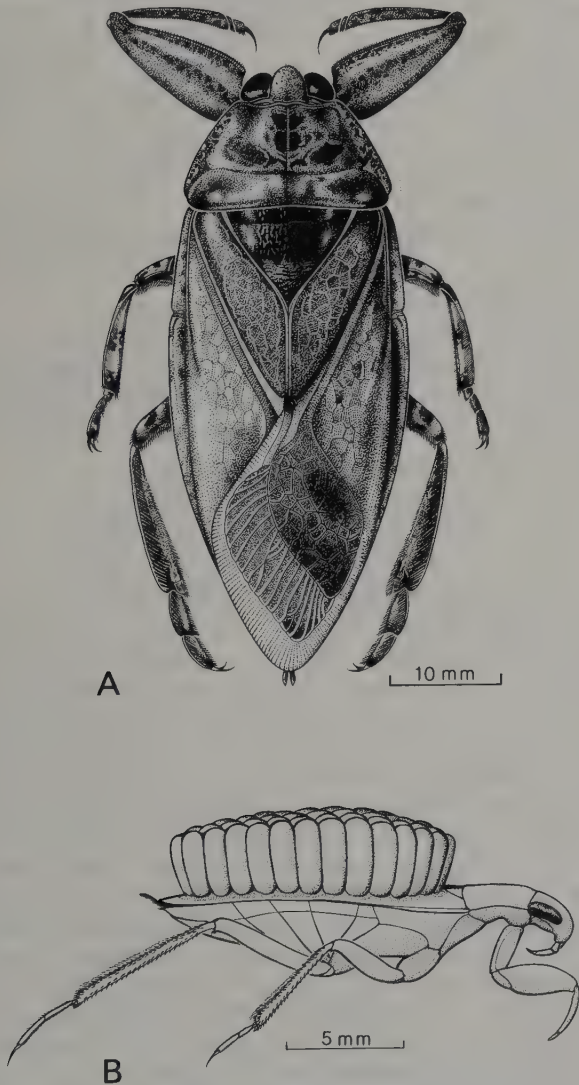


Fig. 30.55 Belostomatidae: A, *Lethocerus insulanus*; B, *Diplonychus rusticus*, ♂, carrying eggs. [S. Monteith]

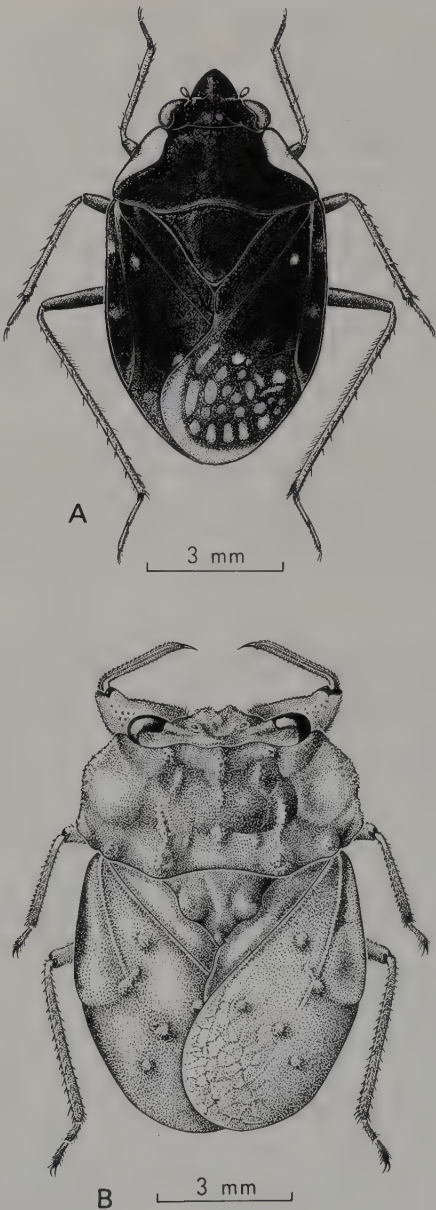


Fig. 30.56 A, *Megochterus nasutus*, Ochteridae; B, *Nerthra nudata*, Gelastocoridae. [S. Monteith; T. Nolan]

face. *Ochterus australicus*, the commonest species, is 3.5 mm long and dark brown with paler brown pronotal flanges. *Megochterus nasutus* is a handsome species about 9 mm long occurring in Qld, Tas. and W.A. [Kormilev 1971; Lansbury 1981; Baehr 1989]

64. Gelastocoridae (toad bugs; Fig. 30.56B). All 23 Australian species belong to the cosmopolitan genus *Nerthra* (NERTHRINAE). Most species live on muddy or sandy banks or shores or damp rock faces, where their colour merges with the background, or just under water; but some are found in debris or soil remote from water, particularly in rainforest. *N. plauta* has been burnt out of spinifex in the semiarid region of S.A. All are predacious. Nymphs and adults hop actively and pounce on their prey. Even macropters have not been seen to fly. [Todd 1960]

Superfamily CORIXOIDEA

65. Corixidae (Figs 3.7B; 30.57A, B). Water-boatmen are predacious, feeding mainly on insect larvae in bottom ooze. They find their prey using their fore tarsi which are hair-fringed and modified into cultrate, scoop-like or cylindrical *palae*. The mid legs are used to cling to the substrate. The hind legs have fringes of long hairs on the tibiae and tarsi and are used for swimming. DIAPREOCORINAE have a bladed ovipositor, ocelli and the hind tarsi fringed with additional cuticular blades. The

subfamily is known from the Jurassic of Europe and Central Asia but is now restricted to New Zealand and the southern half of Australia. *Diaprepocoris* (3 spp.) is the only Australian genus. MICRONECTINAE are much smaller in size than other corixids and are represented by 14 species of the widespread *Micronecta*. CORIXINAE are represented by *Sigara* (*Tropocorixa*) (7 spp.), the predominantly Australian genus *Agraptocorixa* (6 spp.) and *Cymatia* (1 sp.). [Wróblewski 1970; Lansbury 1983, 1984]

Superfamily NAUCOROIDEA

66. Naucoridae (Figs 30.54C, D). Naucorids resemble belostomatids but are considerably smaller (less than 11 mm long) and lack discernible venation on the membrane. Most species are active predators in weedy parts of ponds or slow running waters. The Australian fauna is very depauperate, lacking Ambrysinae, Limnocorinae, Laccocorinae, Cryphocricinae, Cheirochelinae and Potamocorinae. In the NAUCORINAE, *Naucoris* (5 spp.) can be recognised by their broad triangular fore femora. APHELOCHEIRINAE are considered by some authors to be a separate family. *Aphelocheirus australicus* is the only Australian species and has both the fore and mid legs cursorial and antennae partially visible from above. [La Rivers 1971; Polhemus 1984; Lansbury 1985a]

Superfamily NOTONECTOIDEA

Notonectoids have a strongly, transversely arched body; fore wing membrane short or absent. Families are predacious.

Key to the Families of Notonectoidea Known in Australia

- Hind legs oar-like (Fig. 30.57D), with a single claw; hind tibiae flattened, with a clearly visible fringe of long hairs; fore wings with a short membrane; abdomen with a broad, median ventral keel; more than 4 mm long **Notonectidae**
 Hind legs not oar-like (Fig. 30.57C), with 2 claws; hind tibiae cylindrical, hair fringe not visible macroscopically; fore wings lacking a membrane; abdomen with a fine, laminate ventral keel on segments 2–6; less than 4 mm long **Pleidae**

67. Notonectidae (Figs 3.7A; 30.57D). The back-swimmers are easily recognised by their convex dorsal surface, keeled abdominal venter and large, reniform eyes which occupy most of the side of the head. The fore legs are raptorial and the hind legs long, with well-developed fringes of swimming hairs. Notonectids are conspicuous members of the aquatic fauna as they frequently swim close to the surface. NOTONECTINAE are represented by *Enithares* (4 spp., with *E. woodwardi* the most widespread), *Notonecta handlirschi* from W.A., and *Nychia sappho* which occurs from northern Australia to Malaysia. The ANISOPINAE are represented by the Old World *Anisops* (30 Australian spp., some endemic) and the endemic *Parnisops* and *Walambianisops*. [Lansbury 1964–85b]

68. Pleidae (Fig. 30.57C). These are small (less than 2 mm long) back-swimmers with a punctate and/or reticulate pattern on the pronotum, and the hemelytral membrane vestigial or absent. They are relatively poor swimmers preferring to walk over or through the thick, submerged vegetation. Australian species belong to *Pleas* s.l. They are frequently abundant in the tropical north in swamps and lakes and often come to light.

Infraorder CIMICOMORPHA

by G. F. GROSS and G. CASSIS

The limits of this infraorder and the relationships of some of the included families are still subject to discussion (Schuh 1986a). The group is considered to be monophyletic on the basis of the following characters: fore wings usually with a costal fracture, hind wings usually with radius and media fused distally and subcosta often well developed; eggs with a distinct operculum with the aeromicropylar system when present arranged around the operculum; accessory salivary glands vesicular. The loss of the spermatheca is also characteristic of the Cimicomorpha, and sperm is received and retained in other ways (Davis and Usinger 1970), although Reduvioidea are considered to have pseudospermathecae. Pleurally disposed (diastomal) scent gland orifices and abdominal trichobothria (in extralimital Pachynomidae and some Anthocoridae) are features shared with Pentatomomorpha. Many of the families contain species which prey on other arthropods; Cimicidae, Polycetenidae and triatomine Reduviidae are haematophages of vertebrates.

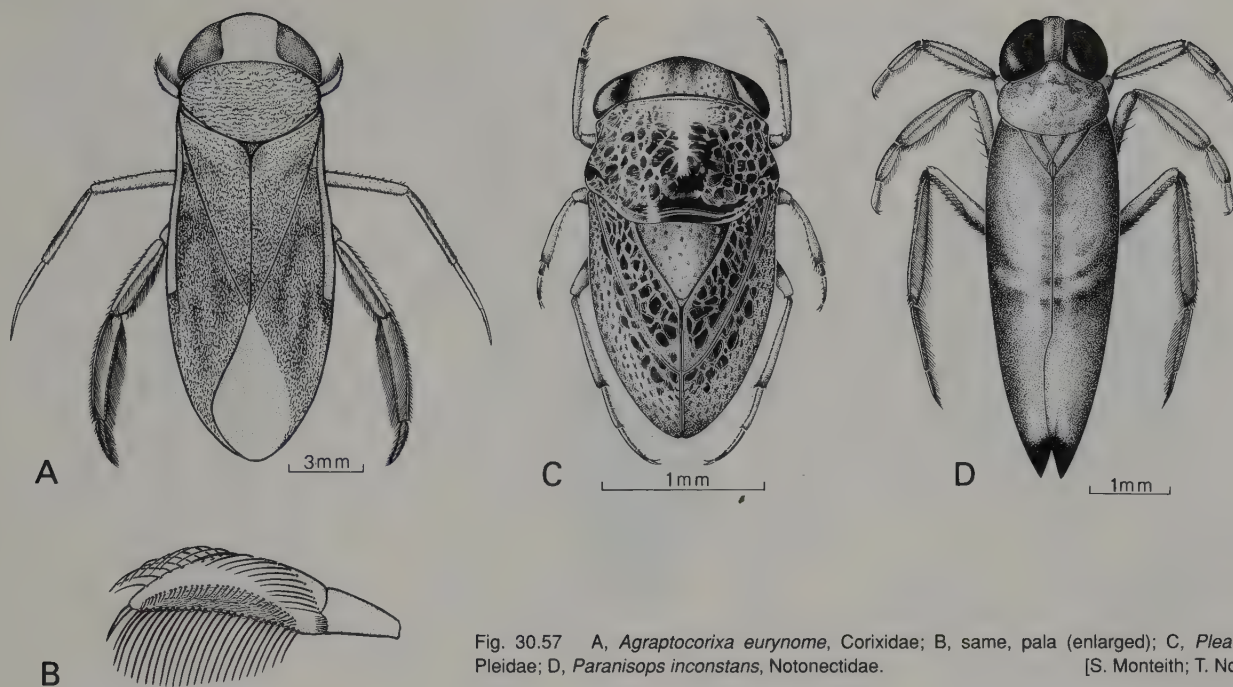


Fig. 30.57 A, *Agraptocorixa eurynome*, Corixidae; B, same, pala (enlarged); C, *Plea* sp., Pleidae; D, *Paranisops inconspicua*, Notonectidae.
[S. Monteith; T. Nolan]

Superfamily CIMICOIDEA

by G. F. GROSS and G. CASSIS

The limits of this superfamily are conjectural, its members being grouped for the most part on the basis of extra-

genital insemination, fertilisation in the vitellarium and pre-ovipositional embryogenesis. Eggs lack micropyles.

Key to the Families of Cimicoidea Known in Australia

1. Eyes absent; with comb-like structures (ctenidia) on head and/or thorax; micropterous; elongate ectoparasites of bats (Fig. 3.25B) **Polyctenidae**
- Eyes present; ctenidia absent; body form varied and usually macropterous but, if ectoparasitic, then body oval and parasites of birds or mammals other than bats 2
- 2(1). Body oval (Fig. 30.58A), flattened; fore wings reduced to transverse scales; pronotum anterolaterally and laterally expanded; clypeus apically expanded; obligatory blood-suckers of vertebrates, including humans **Cimicidae**
- Body, fore wings, pronotum and clypeus not as above; not obligatory blood-suckers 3
- 3(2). Hemelytron without a cuneus (Figs 30.58C, D); labium 4-segmented; ♂ claspers symmetrical; body more than 6 mm long **Nabidae**
- Hemelytron (except in some brachypters) with a cuneus; labium apparently 3-segmented; ♂ claspers usually asymmetrical; body usually less than 6 mm long (Fig. 30.58B) **Anthocoridae**

69. Anthocoridae (Fig. 30.58B). Anthocorids or flowerbugs are usually small (2–5 mm long) and dark brown. Most are fully winged but brachyptery is known. A cuneus is present as in Miridae, from which they differ in having ocelli, an apparently 3-segmented labium and a usually veinless hemelytral membrane. They are most conveniently treated for the present as a single family despite probably being paraphyletic (Schuh 1986a). Haemocoelic insemination is known for all Anthocoridae except Lasiochilinae. The digestive and male internal reproductive systems of a number of Australian species have been studied by Postle and Woodward (1988).

Most species feed on insect eggs or the haemolymph of other small arthropods. A few extralimital species have been recorded feeding on plant material, including pollen (Carayon and Steffan 1959). They occur on plants, in leaf

litter or in the nests and burrows of birds and mammals (Kelton 1978). The family is most diverse in the wet Tropics and all 3 subfamilies occur in Australia. Of the ANTHOCORINAE *Orius armatus* and *O. tantillus* prey on the eggs of *Helicoverpa* and other pest Lepidoptera on sorghum and other crops in northern Australia (Woodward and Postle 1986). LASIOCHILINAE are represented by *Lasiochilus femoralis*. Most Australian LYCTOCORINAE belong to *Cardiastethus* and *Physopleurella*. The introduced *Xylocoris flavipes* is sometimes found in stored grain or peanuts as a predator of pest insects. *Lyctocoris campestris* has been recorded in several countries as a facultative though persistent blood-sucker of humans and other mammals. [Gross 1954–57; Carayon 1972; Woodward 1977]

70. Cimicidae (Figs 30.13, 58A). Cimicids are highly

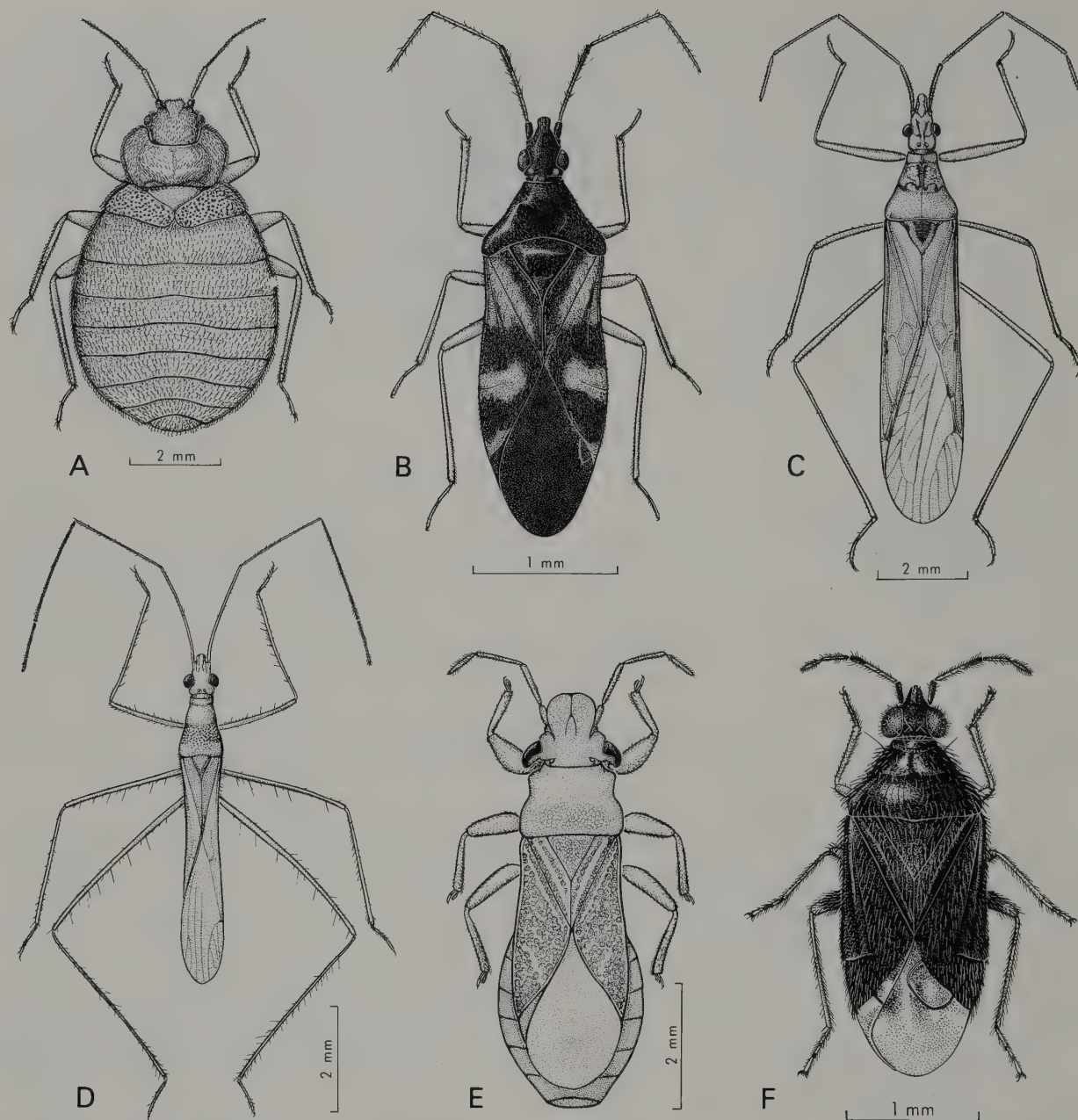


Fig. 30.58 A, *Cimex lectularius*, Cimicidae; B, *Plochiocorella elongata*, Anthocoridae; C, *Nabis kinbergii*, Nabidae; D, *Arbela telomi*, Nabidae; E, *Thaumastocoris australicus*, Thaumastocoridae; F, unidentified species of Isometopinae, Miridae. [S. Monteith]

modified, flightless, flattened ectoparasites which feed on the blood of mammals (especially bats) or birds (Usinger 1966). Being impermanently attached to their hosts, they are more commonly found in roosts and nests. The cosmopolitan bed bug, *Cimex lectularius*, was introduced to Australia with white settlement. Extragenital haemocoelic insemination occurs. The abdominal integument of the female is perforated by the male during copulation and sperm is released into the spermalège opening on S5. Sperm migrates through the haemocoel and penetrates the walls of the seminal conceptacles at the base of the lateral oviducts where it is stored prior to fertilisation.

71. Polyctenidae (Fig. 3.25B). These are small ectopar-

asites of bats in tropical regions. They lack eyes, ocelli, hind wings and ovipositor; and have short, coriaceous fore wings. Comb-like rows of flattened spines (ctenidia) on the body are analogous to those of some Siphonaptera. Polyctenids are viviparous, the young being born at an advanced stage, and differing markedly from the adults; 2 ecdyses occur after birth. Two species are known from North Qld: *Adroctenes magnus* is parasitic on *Taphozous*, and *Eoctenes intermedius* on *Hipposideros diadema*. [Ferris and Usinger 1939; Maa 1964]

72. Nabidae (Figs 30.58C, D). This is a cosmopolitan family of predacious bugs which are usually larger in size than other cimicoids. Eggs are oviposited into grass

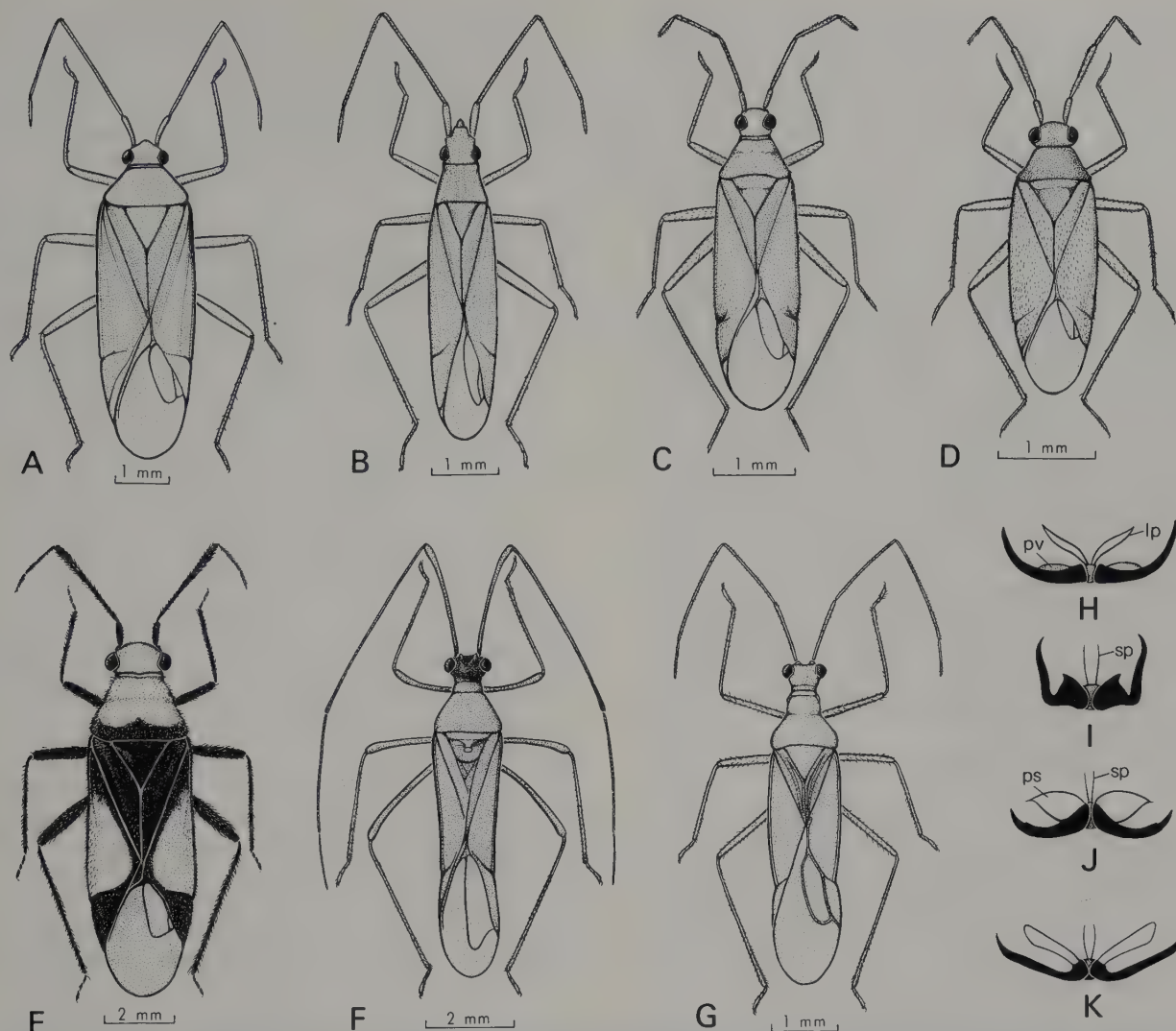


Fig. 30.59 Miridae: A, *Creontiades dilutus*; B, *Trigonotylus doddi*; C, *Nesidiocoris tenuis*; D, *Tytthus mundulus*; E, *Trilaccus nigroruber*; F, *Helopeltis australiae*; G, *Felisacus glabratus*; H-K, pretarsal structures: H, *Trigonotylus doddi*, Mirinae; I, *Trilaccus nigroruber*, Deraeocorinae; J, *Helopeltis australiae*, Bryocorinae; K, *Nesidiocoris*, Bryocorinae.

[S. Monteith]

lp, lamellate parempodium; pv, pulvillus; ps, pseudopulvillus.

stems. Haemocoelic insemination occurs in Prostemmaeinae (Carayon 1954). This and the structure of the egg (Cobben 1968) suggest a closer relationship with Cimicoidea than to Reduvioidea. PROSTEMMATINAE are represented by *Alloeorhynchus*, *Phorticus* and *Prostemma*, and NABINAE by *Gorpis*, *Arbela*, *Stenonabis* and *Nabis*. *Nabis kinbergii* (misidentified in earlier Australian works as the cosmopolitan *N. capsiformis*) is abundant and widespread in Australia and some adjacent areas. A key to genera is given by Woodward (1982) and modified in Woodward and Strommer (1982). [Kerzhner 1969, 1981; Lattin 1989]

Superfamily MIROIDEA

by G. F. GROSS and G. CASSIDY

Miroidea have a 4-segmented labium and a cuneus in the fore wing. The extralimital Microphysidae are tentatively

considered the sister group of the Miridae although they share some features with Anthocoridae (Štys 1962).

73. Miridae (Figs 30.5C, 6E, 58F, 59, 60). This is the largest family of Australian Heteroptera with the majority of species undescribed. Most are phytophagous but many prey on small, soft-bodied insects or insect eggs. Some species feed on both plants and insects, and others are mycetophagous (Kullenberg 1947). Some phytophagous species are injurious to crops, while other predators attack pest insects. The family is characterised by mesofemoral and metafemoral trichobothria, 1 or 2 cells in the fore wing membrane, and specialised male and female genitalia. Species are 2–6 mm long and mostly yellow, green, brown or black, though some are attractively marked. Some species are wing polymorphic or wholly brachypterous. In Australia a high proportion of species are ant mimics, and a few species possibly mimic braconid wasps. The ant mimics have evolved independently in

several subfamilies and tend to have vividly marked black and white, or brown and yellow wings giving the impression of a petiole and abdomen. In some the resemblance has been taken further by a basally constricted abdomen, elongated legs and a modified head.

A satisfactory subfamily and tribal classification has yet to be provided (cf. Reuter 1910; Carvalho 1955–60; Schuh 1974, 1975, 1976, 1984). The classification adopted here most closely follows Schuh.

The Miridae comprise four major groups of subfamilies (Schuh 1976, 1986a; Schuh and Schwartz 1984). Iso-metopinae, Psallopinae and Cylapinae have a subapical tooth on the tarsal claws; Orthotylinae and Phylinae lack a pronotal collar and have a characteristic arrangement of the femoral trichobothria; Mirinae and Deraeocorinae possess a secondary gonopore in the male and have similar female genitalia; and Bryocorinae have distally dilated tarsi with long guard setae or pseudopulvilli arising from the unguitractor plate.

Key to the Subfamilies of Miridae Known in Australia

1. Ocelli present ISOMETOPINAE
Ocelli absent 2
- 2(1). Parempodia lamellate (Figs 30.59H, 60A, B) 3
Parempodia setiform (Figs 30.59I, 60C–F) 5
Parempodia absent BRYOCORINAE-Bryocorini
- 3(1). Parempodia divergent apically (Figs 30.59H, 60A)
..... MIRINAE
Parempodia convergent apically (Figs 30.59K, 60B)
..... 4
- 4(3). Body with at least one band of flattened, silky setae
..... PHYLINAE-Pilophorini
Body without any bands of flattened silky setae
..... ORTHOTYLINAE
- 5(2). Pseudopulvilli (Fig. 30.60C) or pulvilli (Fig. 30.60D)

- present 6
Pseudopulvilli and pulvilli absent (Figs 30.60E, F)
..... 7
- 6(5). Pronotum with rounded, neck-like collar (Fig. 30.59G); pulvilli, if present, very large, fused to inner surface of claws; if pulvilli absent then pseudopulvilli present (Figs 30.59J, 60C)
..... BRYOCORINAE (pt)
Pronotum not as above (Fig. 30.59D); pulvilli present (Fig. 30.60D), usually small, attached to ventral surface of claws; pseudopulvilli absent
..... PHYLINAE (pt)
- 7(5). Claws thickened or toothed at base (Figs 30.59I, 60E), without subapical tooth DERAECORINAE
Claws slender, without thickened or toothed base, often with subapical tooth (Fig. 30.60F) 8
- 8(7). Rounded pronotal collar usually present; tarsi usually 3-segmented; wing membrane with 2 cells
..... CYLAPINAE
Rounded pronotal collar absent; tarsi 2-segmented; wing membrane with 1 cell PSALLOPINAE

ISOMETOPINAE differ from other mirids in possessing ocelli. Species often prey on mealybugs and scale insects. *Eurocrypha thanatochlamys* is the only Australian species. [Ghuri and Ghauri 1983]

PSALLOPINAE are represented by several undescribed species of *Psallops*.

CYLAPINAE are considered to be mycetophagous. Cylapini contain beetle-like (coleopteroid) species of *Carvalhoma* and *Schizopteromiris* (J. A. Slater and Gross 1977; Schuh 1986b). Bothriomirini are represented by an undescribed species, which possibly belongs to *Bakeriola*. Fulviini are represented in Australia by about a dozen species with conical heads and speckled appearance.

In ORTHOTYLINAE the parempodia are lamellate,

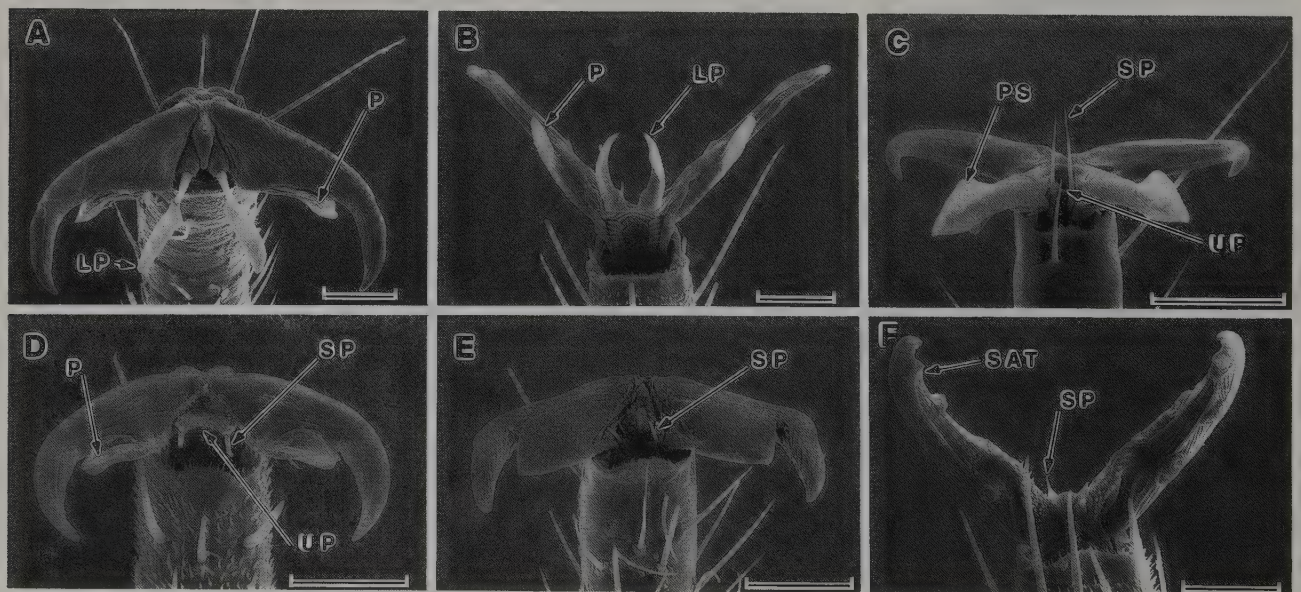


Fig. 30.60 Miridae: Pretarsal structures. A, *Pseudopantilius* sp., Mirinae (scale = 50 μ m); B, *Halticus* sp., Orthotylinae (scale = 20 μ m); C, *Setocoris* sp., Bryocorinae-Dicyphini (scale = 50 μ m); D, *Sejanus* sp., Phylinae (scale = 50 μ m); E, *Deraeocoris* sp., Deraeocorinae (scale = 20 μ m); F, *Fulvius* sp., Cylapinae (scale = 20 μ m).

LP, lamellate parempodium; SP, setiform parempodium; PV, pulvillus; PS, pseudopulvillus; SAT, subapical tooth; UP, unguitractor plate.

[C. D. Beaton]

recurved and strongly convergent apically; pulvilli are present; and the pronotum usually lacks a distinct collar. There are only a few species of Halticini, including *Halticus minutus* which is more common in the Pacific as a pioneer species. Ant-mimetic genera such as *Myrmecoridea* and *Myrmecoroides* whose species not only are colour-marked so as to resemble ants, but also have the base of the abdomen constricted to give the impression of a petiole, form an endemic, monophyletic group. Most Orthotylini belong to the widespread genera *Melanotrichus*, *Orthotylus*, *Pseudoloxops* and *Zanchius*. *Coridromius variegatus* is a squat, speckled species resembling a geocorine lygaeid. The predacious *Cyrtorhinus lividipennis* is widespread in the south-western Pacific region. *Kirkaldyella* with several black or brown, rugose species occurs only in Australia and New Guinea. In the endemic Austromirini (*Austromiris*, *Dasymiris*, *Porphyrodema* and *Zanessa*) the frons is longitudinally sulcate, porrect and protrudes between the antennae.

PHYLINAE are usually small (2–3 mm), whitish, yellow, brown or black mirids with setiform parempodia and pulvilli which arise from the ventral surface of the claw; most species lack a pronotal collar. Pilophorini (*Pilophorus*, *Paramixia*) and Hallodapini (*Acrorrhinium*, *Hallodapus* and several undescribed genera) are ant-mimetic and represented by only a few species. Leuco-phoropterini have minute genitalia (Schuh 1986a) and are often convincing ant mimics, though this mostly does not extend past a colour mimicry. They are particularly well represented in Australia with most Australian species belonging to *Sejanus* (Carvalho and Gross 1982). This tribe also contains *Tytthus mundulus* which preys on the eggs of the sugar cane delphacid, *Perkinsiella saccharicida*. Phylini are represented by widely distributed genera such as *Campylomma*, *Chlamydatus*, *Plagiognathus*, *Psallus* and *Sthenarus* and several undescribed genera. *Campylomma livida*, the (apple) dimpling bug, is a small, pale species which is widely distributed and a pest in some parts of Australia. [Schuh 1984]

MIRINAE are larger than most other mirids and usually have clearly visible, lamellate, divergent parempodia. Pulvilli are present and attached to the ventral surface of the claws. Mirini have a distinct, raised pronotal collar and an opaque corium and clavus. There are many endemic genera in Australia, including *Austrocapsus* (2 spp.), *Pseudopantilius* (1 described and several undescribed spp.) and *Niastama* (3 spp., occasionally minor pests on apples etc.). *Sidnia kinbergi* is a pest of lucerne and other crops. Important pests belonging to widespread genera are *Calocoris norvegicus*, the potato capsid, which is well established in Tas., and *Creontiades dilutus* (= *Megacoelum modestum*), a pest of stone fruits and cotton. Hyalopeplini are large like Mirini but differ in having the fore wings completely transparent between the veins. They are mostly tropical (Carvalho and Gross 1979). Stenodemini are pale, linear, with a flattened pronotal collar; they feed on grasses (Carvalho and Gross 1980).

DERAEOCORINAE are often robust, heavily punctate and densely setose; the parempodia are setiform and there are no pulvilli. Teratophylini prey on Thysanoptera and are

represented in Australia by undescribed species of *Teratophylloides*. Deraeocorini prey on other Hemiptera. *Deraeocoris* is cosmopolitan with *D. signatus* abundant on sorghum. Saturniimirini are colourful black and red mirids with a transverse impression on the pronotum; they are restricted to Australia (where there are 5 genera) and New Guinea. *Trilaccus* is sometimes common on potato and Cape gooseberry plants in Qld.

BRYOCORINAE are a heterogeneous group with two of the three recognised tribes represented in Australia. Dicyphini include one group of genera comprising delicate insects associated with plants that have glandular trichomes and/or toxic compounds such as alkaloids. Species of the endemic genus *Setocoris* are brightly coloured with red, green and black, live on the insectivorous plants *Drosera* and *Byblis*, and prey on insects trapped on the sticky hairs of the plants. The widespread species, *Engytatus nicotianae* and *Nesidiocoris tenuis*, which feed on tobacco and other solanaceous plants, are also known from Australia. *Pachypeltis*, *Pachypeltopsis*, *Ragwelellus* and *Rayieria* are numerous in tropical and subtropical regions. *Felisacus glabratus* feeds on ferns. Some Dicyphini are more ovate with a greatly swollen scutellum. Eccritotarsini are represented in Australia by the widespread *Bromeliaemiris puncticollis*.

Superfamily TINGOIDEA

by G. F. GROSS and G. CASSIS

The Tingoidea are probably the sister group of the Miroidea as both are primarily phytophagous with a declivous head, 4-segmented labium, well-developed bucculae and ovipositor, and similar seminal sacs in females. Both usually lack ocelli, the hind wing hamus and first abdominal spiracles. Tingoids are highly derived, with distinctive modifications of the dorsum, and bizarre, spinose nymphs. The extralimital Vianaididae are myrmecophilic, coleopteroid and have vestigial eyes. They are considered by some to be a subfamily of the Tingidae. The extralimital Joppeicidae are placed in this superfamily because of similarities in the hemelytron, metathoracic glands and mode of fecundation (Davis and Usinger 1970). [Drake and Davis 1960]

74. Tingidae (Fig. 30.61). These are known as lace bugs because of the raised reticulations on the pronotum and fore wings. The head and pronotum often bear prominent spiny or inflated processes or carinae. Tingids are phytophagous and often gregarious near the egg masses from which they have emerged. Péricart (1983) considered the classification and morphology of the family and Lee (1969) the immature stages and male genitalia. TINGINAE (140 spp.) are more morphologically diverse than CANTACADERINAE (8 spp.). Very little is known of the biology of Australian species. Endemic species have been captured on *Sarcopetalum*, *Eucalyptus*, *Casuarina*, *Grevillea*, *Dodonaea*, *Thryptomene* and *Notelaea*, and also obtained from moss and leaf litter. Two species are found with ants, *Allocader leai* with *Amblyopone australis* in Tas. and *Lasiacantha leai* with *Iridomyrmex conifer* in W.A. *Froggattia olivinia*, though an endemic,

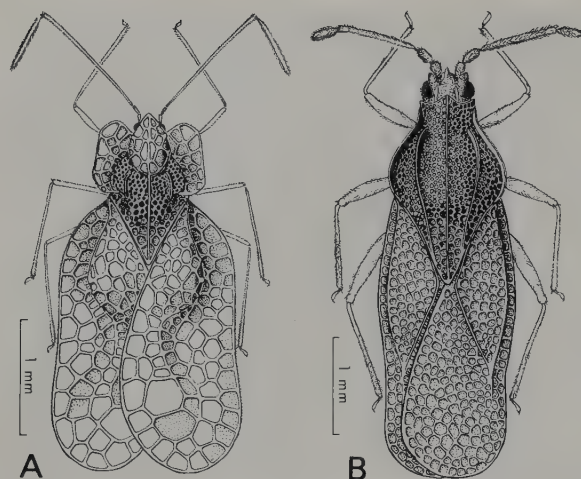


Fig. 30.61 Tingidae: A, *Stephanitis queenslandensis*; B, *Teleonemia scrupulosa*. [S. Monteith]

forms flower galls on the introduced olive. *Teleonemia scrupulosa* was introduced from Central America (via Fiji) to Australia to attack lantana (Harley and Kassulke 1971) and is now common in Qld and northern N.S.W. The introduced *Stephanitis pyrioides* and *S. rhododendri* are pests of azaleas and *Kalmia*. [Drake and Ruhoff 1960, 1965]

Superfamily THAUMASTOCOROIDEA

by G. F. GROSS, J. A. SLATER and L. HILL

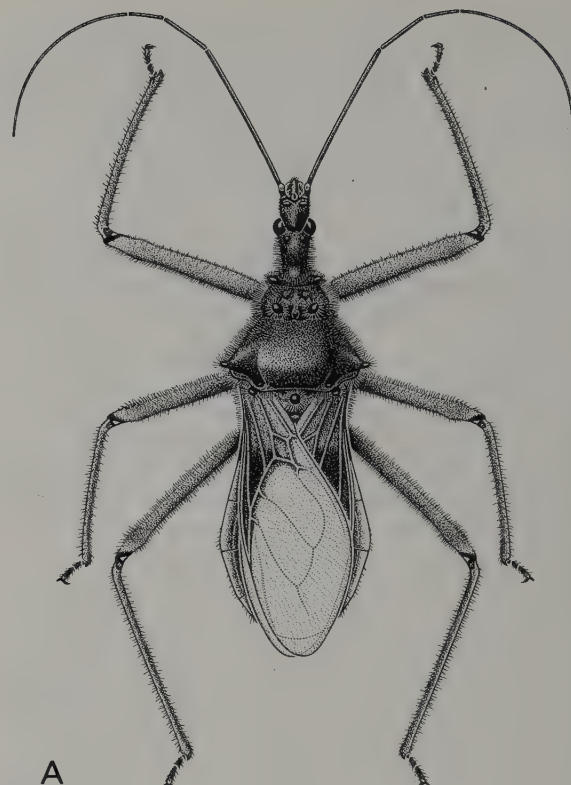
Most authors agree that this group belongs in the Cimicomorpha (Drake and Slater 1957; Štys 1962; Schaefer 1969) but occupies an isolated position. Cobben (1968) believed that they are not Cimicomorpha but a separate, major branch of Heteroptera.

75. Thaumastocoridae (Fig. 30.58E). Thaumastocorids have a flattened body, ocelli, pedunculate eyes, a 4-segmented labium, highly asymmetrical male genitalia (lacking one or both parameres), reduced female genitalia and setiform parempodia. The family has a relictual, Gondwanan distribution. THAUMASTOCORINAE occur only in Australia (3 genera) and India (1 species) and the Xylastodorinae in South America, Cuba and Florida. J. A. Slater (1973) discussed the feeding habits, taxonomy and phylogeny of the family. All are phytophagous having been recorded from *Acacia*, *Banksia*, *Elaeocarpus*, *Eucalyptus* and *Melaleuca*. *Baclozygum depressum* severely damages adult leaves of *Eucalyptus globulus* in Tas. (L. Hill 1988).

Superfamily REDUVIOIDEA

by G. F. GROSS and M. B. MALIPATIL

The Reduvioidea are considered by most authors to be Cimicomorpha, with their closest allies perhaps the Tingoidea and Thaumastocoroidea (Popov 1981). Others (e.g. Cobben 1968), on the basis of the structure and development of the egg, believe that the Reduviidae at least (Pachynomidae have nabid-like eggs) form a distinct major branch (Reduviomorpha) of the Heteroptera.



A

10 mm



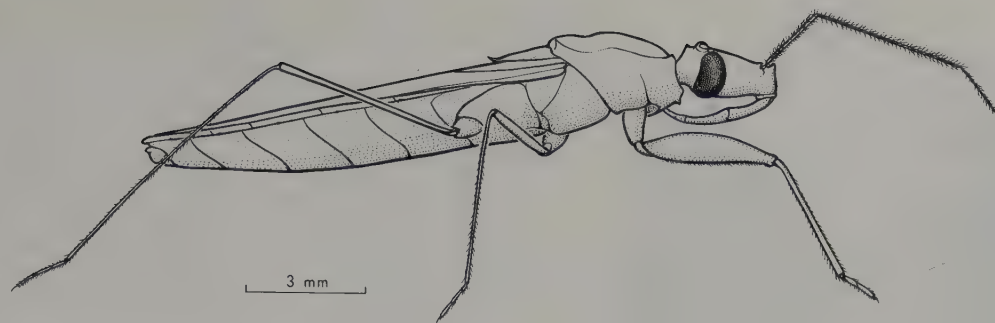
B

2 mm

Fig. 30.62 *Pristhesancus plagipennis*, Reduviidae.

[A by S. P. Kim; B by M. Quick]

76. Reduviidae (assassin bugs; Plate 3, I–K; Figs 30.8A, 11C–D, 62–64). This large family is well represented in Australia, being most diverse in tropical regions. All species are predacious. Most attack other arthropods but the Triatominae (represented in Australia by one species) feed on the blood of mammals and birds. A few of the larger species which prey on arthropods can inflict painful bites on humans (Southcott 1986). Reduviids are diverse in appearance and generally large in size; wing polymorphism occurs in some species. Many can produce sound by rubbing the short labium against a transversely striated groove on the prosternum. In some subfamilies the fore and sometimes mid tibiae

Fig. 30.63 *Oncocephalus confusus*, Reduviidae.

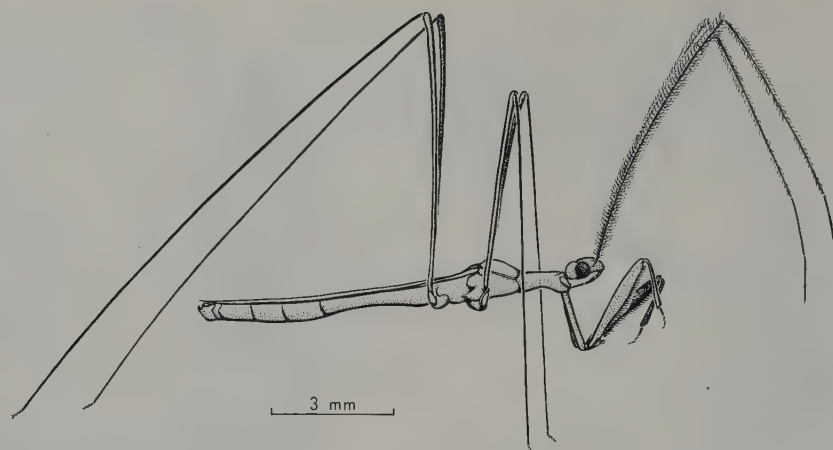
[S. Monteith]

have expanded, spongy, setose pads (*fossulae spongiosae*) which assist in holding prey. In other subfamilies the tibiae and femora of the fore legs are spiny and opposable to hold the prey. Glandular structures are more diverse in Reduviidae than in any other heteropteran family (Staddon 1979). Louis and Kumar (1973) discussed the comparative morphology of the alimentary and reproductive organs.

Fewer than half of the nearly 30 subfamilies (China and Miller 1959; Davis 1969) occur in Australia.

Key to the Subfamilies of Reduviidae Known in Australia

1. Fore coxae very elongate, at least 4 times longer than wide, reaching or surpassing apex of head; fore legs raptorial, each with tibia and femur opposable and often spinose (Fig. 30.64) EMESINAE
 - Fore coxae not more than 3 times longer than wide; fore legs not spinosely raptorial 2
- 2(1). Ocelli absent 3
 - Ocelli present 5
- 3(2). Body covered with short, dense pubescence; 1st antennal segment much thicker than following segments TRIBELOCEPHALINAE
 - Body at most only minutely pubescent; 1st antennal segment subequal in thickness to following segments 4
- 4(3). Apex of fore tibia with large, flattened, acute projection on inner surface; pronotum without spines; head and body highly polished VISAYANOCORINAE
 - Fore tibia without such projection; pronotum usually with spines; head and body only slightly polished. SAICINAE
- 5(2). Scutellum short and broad, semicircular in outline or with apex truncate or excised (Plate 3, K) 6
 - Scutellum triangular with apex produced (Fig. 30.62) 7
- 6(5). Fore tarsi 2-segmented; head short in front of eyes; antennae inserted close to eyes; antennae and legs, especially the hind tibiae which may be plumose, with dense long hairs or spines; scutellum short and broad, often almost semicircular in outline, fringed with spines or hairs (Plate 3, K) HOLOPTILINAE
 - Fore tarsi 3-segmented; head produced in front of eyes; antennae inserted a little in front of eyes; antennae and legs with sparse long hairs; scutellum with apex broad and strongly excised medially, laterally and apically with raised keels forming H-shaped structure ECTRICHODIINAE
- 7(5). Hind margin of pronotum produced into a tongue-like process on either side of scutellum; apex of scutellum produced into a hollow spatulate process; body covered with short, rigid, thick setae many of which are hooked apically PHYSODERINAE
 - Hind margin of pronotum not produced into a tongue-like process on either side of scutellum; apex of scutellum not spatulate; pilosity on body not as above 8
- 8(7). Labium appearing 2-segmented and produced over mesosternum; pronotum with 2 or 4 longitudinal, sinuate, pilose keels TEGEINAE
 - Labium distinctly 3-segmented and just reaching prosternum (Fig. 30.62); if pronotum with longitudinal keels then latter not pilose 9
- 9(8). Head without a transverse sulcus immediately behind eyes; ocelli widely separated and placed almost on sides of head TRIATOMINAE
 - Head with a curved transverse sulcus immediately behind eyes (Fig. 30.62); ocelli separated at most by little more than space between eyes 10
- 10(9). Neck region of head long; corium with an apical quadrangular cell usually about as long as wide (Fig. 30.62) HARPACTORINAE
 - Neck region of head short; cell on corium, if present, 3-, 5- or 6-sided 11
- 11(10). Fore tibia without a pilose, spongy pad (*fossula spongiosa*) apically, or if such a structure present on tibia then pronotum with strongly developed dorsal spines; if pronotum with a transverse groove then broad and ill defined (Fig. 30.63) STENOPODAINAE
 - Fore tibia more robust and with a *fossula spongiosa*, if not then pronotum unarmed; latter always with a sharply defined transverse groove 12
- 12(11). Frequently brachypterous or apterous; *fossula spongiosa* of fore tibia often extends from apex to halfway along tibia (Plate 3, I, J) PEIRATINAE
 - Usually fully winged, if brachypterous and if a *fossula spongiosa* present on fore tibia then only subapically REDUVIINAE

Fig. 30.64 *Ploiaria regina*, Reduviidae.

[S. Monteith]

The HARPACTORINAE is the largest subfamily; species are mostly diurnal and found on plants. *Pristhesancus* and *Helonotus* (Malipatil 1986a, b) are represented in Australia and New Guinea; the 'bee-killer', *P. plagipennis* reaches 25 mm. Smaller species include *Gminatus nigroscutellatus*, *Leana australis* and *Havithus rufovarius*. *Dicrotelus* and its allies are strongly spined. Species of *Coranus* are frequently brachypterous, and ground living (Malipatil 1986c).

PEIRATINAE are mostly robust, nocturnal, ground-living species. *Peirates* includes several brown or black species, often with a yellowish patch at the base of the hemelytron. *Ectomocoris decoratus* (Plate 3, I), an orange and black species with both macropterous and apterous forms, has been reported as 'biting' forestry workers in Qld.

The TEGEINAE are represented only by *Tegea atropicta* which is a specialised termite predator, piercing the gallery walls with its elongate rostrum (Casimir 1960). REDUVIINAE (= Acanthaspidinae) are represented by about 12 genera, several of which probably should be transferred to other subfamilies. TRIATOMINAE, which suck the blood of vertebrates and in South and Central America transmit a debilitating or sometimes fatal trypanosomiasis (Chagas' disease), are represented by *Triatoma leopoldi* in Cape York Peninsula (Monteith 1974).

There is one dubious record of PHYSODERINAE in Australia. VISAYANOCORINAE are represented by several undescribed species.

STENOPODAINAE are well represented by rather elongate, medium to large sized, yellow to brown, nocturnal species in many genera, the commonest being *Oncocephalus*, *Pygolampis*, *Sastrapada*, *Thodelmus* and *Centrogonus*. The ECTRICHODIINAE, which are nocturnal and ground-living predators of millipedes, are represented in Australia by 8 small, colourful species in as many genera. The slender SAICINAE occur only in tropical Australia where they are represented by *Polytoxus* and *Micropolytoxus*. TRIBELOCEPHALINAE (*Opisthoplatys*, 2 spp.) are dull coloured, nocturnal and occur in plant debris.

HOLOPTILINAE have plumose hind tibiae and sometimes a ventral abdominal trichome. Secretions from the tri-

chome are reported to attract and paralyse the ants on which holoptilines prey. The subfamily includes several species of *Ptilocnemus* (Plate 3, K) with very conspicuously plumose hind tibiae; *Ptilocerus* in northern Australia; and *Aradellus* and *Aradelloides* which have short, rod-like hairs (Malipatil 1985).

EMESINAE have raptorial fore legs with very long coxae, and a long and slender body. They prey on small insects. Wygodzinsky (1966) listed 44 Australian species. The best represented genera are *Ploiaria*, *Stenolemus*, the apterous *Bargylia* and the usually apterous *Pseudobargylia*. One of the commoner species is the cosmopolitan *Empicoris rubromaculatus* with a red costal spot.

Infraorder PENTATOMOMORPHA

This is one of the largest groups of Heteroptera. Pentatomomorphs lack a costal fracture in the fore wings and in the hind wings R and M are distally separated and Sc is never well developed. The accessory salivary glands are tubular and the egg lacks a true operculum but an egg burster is present (Leston *et al.* 1954; Cobben 1968). Most of the Pentatomomorpha were recognised early as a distinctive grouping as they have trichobothria spread variously over the body, but they are almost unique (see Cimicomorpha, p. 488) in having pregenital abdominal trichobothria. Aradoidea and *Oxycarenus* (Lygaeidae) lack abdominal trichobothria but do have a number of the other pentatomomorph features. Nearly all Pentatomomorpha are phytophagous; the Aradoidea are mycetophagous and one subfamily of Lygaeidae (Geocorinae) and one small group of Pentatominae (Pentatomidae) have become secondarily predacious.

Superfamily ARADOIDEA

by G. B. MONTEITH and G. F. GROSS

Aradoidea have a number of primitive features (Kumar 1967), including a 2- or 3-layered bulbous ejaculatorius, presence of an ileum, absence of gastric caeca, undifferentiated or only partly differentiated principal salivary

glands, and undifferentiated accessory salivary glands and their ducts. However, they have become highly specialised in other respects in response to mycetophagous habits, including (usually) a strongly flattened body form and elongate stylets (often exceeding the body length) to insert into the fungal mycelia.

77. Aradidae (flat bugs, bark bugs; Fig. 30.65). The family is cosmopolitan with the greatest diversity in rainforests. The long stylets are stored retracted into the enlarged clypeal region of the head as a simple coil or figure-of-eight, the conformation being significant at subfamily level (Lee and Pendergrast 1976). The stylets tap fluids from mycelia or fruiting bodies of wood-decaying fungi and hence aradids are always associated with dead or dying wood, particularly in humid situations.

Typically, aradids are macropterous, highly flattened, reddish brown, and live under loose bark, usually gregariously. However, many species live on the outer surface of sticks and logs on the rainforest floor. These achieve bark crypsis by small size, colour pattern, and often by aptery and fusion and ornamentation of the dorsal body sclerites (Monteith 1982). About half of the Australian species are apterous. Several usually apterous species retain a rare, winged morph with dispersal capacity.

All eight subfamilies (Usinger and Matsuda 1959) are present in Australia. Most species occur along the moist, east coast of Qld which has 147 spp., and the fauna attenuates rapidly to the south (Tas., 10 spp.) and west (W.A., 4 spp.). Three primitive subfamilies are restricted to the Southern Hemisphere. ISODERMINAE include only *Isodermus* with one species in Chile, three in New Zealand and two in Tas. and south-eastern mainland Australia. They are strongly flattened, the head lacks bucculae and a rostral groove, and the wing membranes are deciduous. PROSYMPIESTINAE occur in New Zealand, Australia and perhaps in New Guinea. Four Australian species occur in Tas. and the eastern mainland. All belong to the lygaeid-like *Prosympiestus* and have a curved bristle emerging from the scent-gland orifice. CHINAMYERSIINAE include winged and wingless genera in Australia, New Zealand, New Caledonia and Vanuatu (Monteith 1980). The relict, apterous *Kumaressa*, with 3 spp. in eastern Australia, is closely related to the New Zealand *Tretocoris*.

The five remaining subfamilies are more or less cosmopolitan. ARADINAE are represented by 5 small, macropterous species of *Aradus*, which are widespread in semi-arid regions and often come to light. CALISIINAE (12 spp.) are minute and immediately recognisable by their enlarged scutellum which entirely covers the wings at rest. ANEURINAE (5 spp.) are small, paper-thin, macropterous species lacking a rostral groove.

Most species belong to the MEZIRINAE (80 spp.) and the CARVENTINAE (55 spp.). These two subfamilies have the genal lobes well developed, usually projecting forward on each side of the clypeus. Mezirinae have a well-developed metapleural scent-gland orifice, while Carventinae lack this orifice and have the body covered with a pale, waxy secretion which is highly ornamental. *Mezira* and *Neuroctenus* (Mezirinae) include common species living under bark in non-rainforest habitats but most other

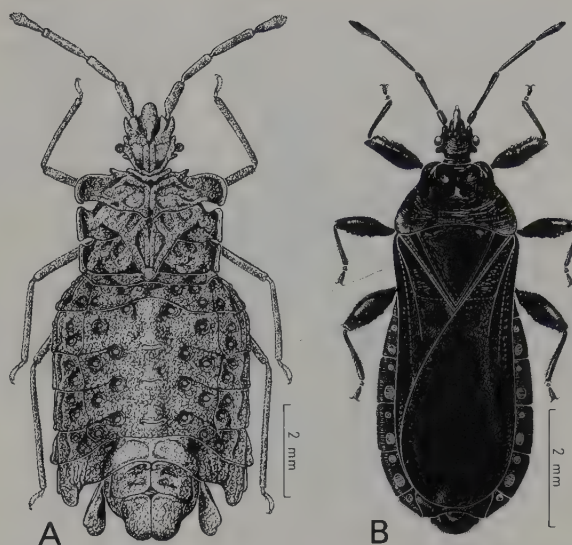


Fig. 30.65 Aradidae: A, *Kumaressa scutellata*; B, *Isodermus planus*.
[S. Monteith, T. Nolan]

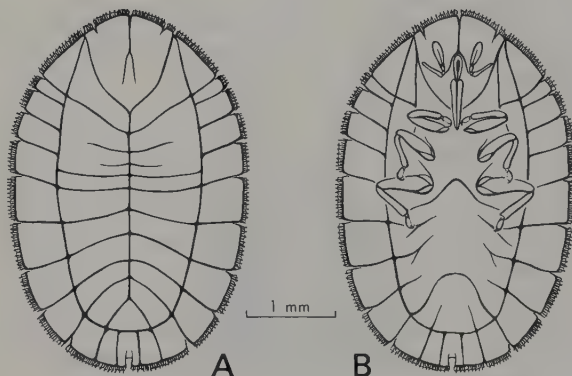


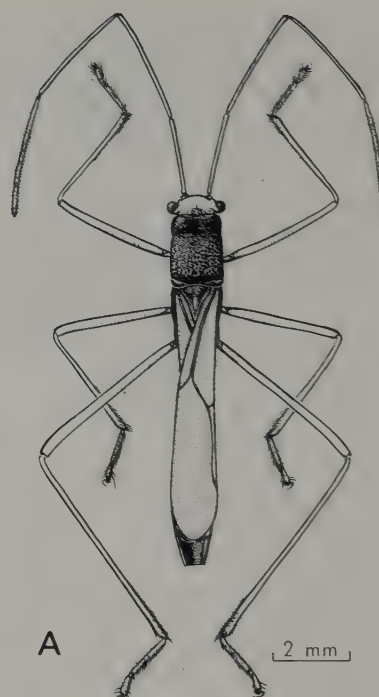
Fig. 30.66 *Termitaradus australiensis*, Termitaphididae: A, dorsal; B, ventral.
[S. Monteith]

species of these two subfamilies are confined to the tropical and subtropical rainforests of north-eastern Qld. An exception is *Aspisocoris termitophilus*, a cylindrical, termitophilous mezirine with reduced eyes, from south-western W.A. Rainforest mezirines include minute, macropterous genera (*Chiastoplonia*, *Glochocoris*, *Clavicornia*), heavy bodied apterous genera (*Drakiessa*, *Chelanoderus*) and, in northern Cape York Peninsula, some wing dimorphic genera (*Caecicoris*, *Usingerida*) which are recent immigrants from New Guinea. The rainforest carventines are apterous except for several species of *Carventus* and include highly convex genera such as *Glyptoaptera* and *Probaticeps* which mimic the rough surface of bark. On Lord Howe I. there are 3 species of the apterous genus *Acaraptera*, which is widespread in the south-western Pacific region but absent from the Australian mainland. [Kormilev and Froeschner 1987]

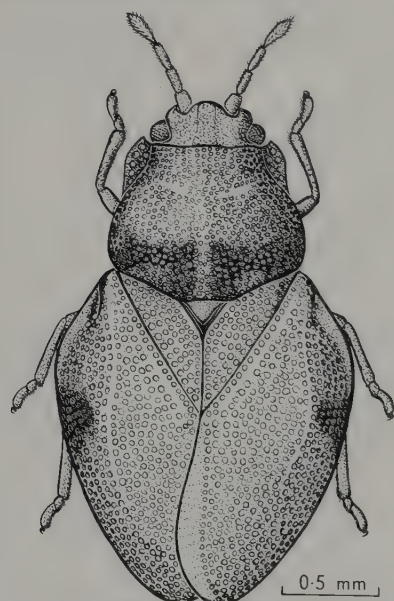
78. Termitaphididae (Fig. 30.66). A very small, circumtropical family of flattened, blind, apterous bugs (superficially resembling some apterous Sternorrhyncha) which live in termite nests. They possess long, coiled

Fig. 30.67 *Monteithocoris hirsutus*, Idiostolidae.

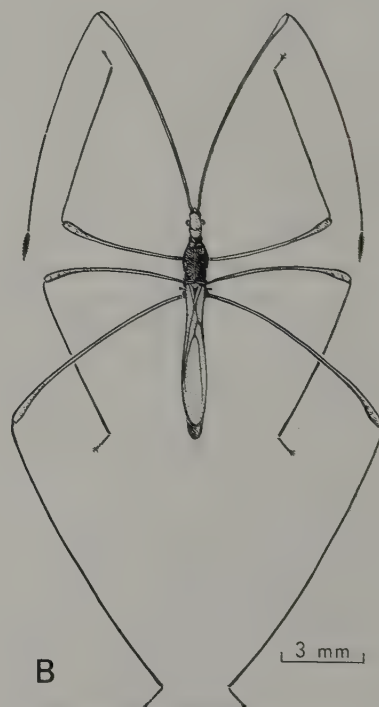
[S. Monteith]



A

Fig. 30.68 *Mcateella* sp., Piesmatidae.

[S. Monteith]



B

stylets like aradids and are assumed to feed on fungal mycelia which abound in termite nests. They lack dorsal abdominal scent gland openings. *Termitaradus australiensis* lives in nests of *Coptotermes acinaciformis* in Qld and N.S.W. [Usinger 1942]

Superfamily IDIOSTOLOIDEA

by J. A. SLATER and G. F. GROSS

79. Idiostolidae (Fig. 30.67). This small and possibly ancient family occurs only in Australia and southern

Fig. 30.69 A, *Phaenacantha australiae*, Colobathristidae; B, *Metacanthus pluto*, Berytidae.

[S. Monteith]

South America. Their habits and food plants are unknown but all species appear to be associated with *Nothofagus* forests. They exhibit some plesiomorphic features in the arrangement of the abdominal trichobothria and articula-

tions of the female genitalia, but in other respects the genitalia of both sexes are quite advanced including the loss of a spermatheca (Schaefer and Wilcox 1969). Idiostolids are ground living, flattened, brown and yellow bugs with a lygaeid- or mirid-like habitus. *Triseus* (2 spp.) occurs in Tas., Vic., northern N.S.W. and southern Qld, and *Montethocoris* (1 sp.) in Tas. [Woodward 1968b]

Superfamily PIESMATOIDEA

by G. F. GROSS

80. Piesmatidae (Fig. 30.68). Though piesmatids superficially resemble tingids, morphological studies have shown that they are Pentatomomorpha most closely rela-

ted to the Lygaeoidea. There are only 4 included genera, *Piesma* in Europe, Africa, Asia and North America, *Miespa* in Chile, *Thaicoris* in South-East Asia and *Mcateella* (4 spp.) in Australia. The only known host plants of *Mcateella* are *Acacia* spp. and *Beyeria leschenaultii*. [Schaefer 1981]

Superfamily LYGAEOIDEA

by G. F. GROSS (Lygaeidae by J. A. SLATER)

There is not yet general agreement on the limits between the Lygaeoidea and the Coreoidea, or whether the Pyrrhocoridae and Largidae are Lygaeoidea or belong to a separate superfamily. [Scudder 1963; Štys 1964, 1967, 1984; Schaefer 1965; Kumar 1968]

Key to the Families of Lygaeoidea Known in Australia

1. Ocelli absent; body more than 5 mm long and with red or yellow ground colour 2
 Ocelli present except in a few forms which are less than 5 mm long and brown or black in colour 4
- 2(1). Usually macropterous, with 6 or more longitudinal veins on membrane of hemelytron (Figs 30.73B, C); hemelytron of brachypters with membrane well developed and with several longitudinal veins 3
 Always brachypterous, with membrane of hemelytron absent or greatly reduced and with no longitudinal veins **Lygaeidae** (pt)
- 3(2). Pronotum with lateral margins usually not reflexed, sometimes reflexed only on anterior lobe; the 3 trichobothria on each side of S5 arranged in a longitudinal row mesad of spiracle; ♀♀ with long ovipositor and S7 cleft in mid-line to receive it (Figs 30.73B, 74A) **Largidae**
 Pronotum with lateral margins reflexed throughout; the 3 trichobothria on each side of S5 arranged in a close group anterior to spiracle; ♀♀ with short ovipositor and S7 without median cleft (Figs 30.73C, 74B) **Pyrrhocoridae**
- 4(1). Legs and antennae long and exceedingly slender, thread-like; apices of femora and usually antennal scape slightly but appreciably swollen; apical antennal segment short, relatively thick, spindle-shaped; body linear (Fig. 30.69B) **Berytidae**
 Legs and antennae robust to slender, but legs never exceedingly slender and thread-like, nor with apices of femora swollen; if antennae exceedingly slender and thread-like, then scape not swollen at apex, and apical segment long and slender; body form varied 5
- 5(4). Antennae longer than body, thread-like, all segments very long and slender; wings long and narrow; membrane of hemelytron with veins absent or obsolescent; abdomen narrowed at base (Fig. 30.69A); 1 Australian sp. **Colobathristidae**
 Antennae not longer than body nor thread-like; form of wings and abdomen varied; many Australian spp. **Lygaeidae** (pt)

81. Colobathristidae (Fig. 30.69A). *Phaenacantha australiae* is the only Australian species of a mainly South-East Asian and tropical South American group. It occurs in large numbers on grasses in coastal Qld and may be a pest of sugar cane. [Štys 1966]

82. Berytidae (stilt bugs; Figs 30.10G, 69B). A small family of phytophagous, delicate bugs with long antennae and legs. *Neides* (2 spp.) occurs in southern Australia. *Protocanthus halei* extends into arid regions. *Metacanthus pluto* feeds on leaves of stinging trees (*Dendrocnide*) in eastern rainforests. [Gross 1950]

83. Lygaeidae (Plate 3, V, W; Figs 2.40; 30.6B, 70–73A). Most species of this large family feed on seeds. A few are sap-sucking, predacious or feed on vertebrate blood. J. A. Slater (1964) catalogued the world fauna and China and Miller (1959) dealt with the subfamily classification.

Key to the Subfamilies of Lygaeidae Known in Australia

1. Suture between S4 and S5 curving forward laterally and not attaining lateral margins of abdomen;

- trichobothria usually present on head (Fig. 30.70) RHYPAROCHROMINAE
- Suture between S4 and S5 not curving forward, attaining lateral margins of abdomen; head without trichobothria 2
- 2(1). Spiracles on abdominal segments 2–7 all located dorsally 3
 At least one pair (and often more) of spiracles on abdominal segments 2–7 located ventrally 5
- 3(2). Clavus at least in part punctate; posterior margin of pronotum not depressed laterad of base of scutellum (Fig. 30.72C) ISCHNORHYNCHINAE
 Clavus impunctate; posterior margin of pronotum depressed between scutellum and lateral angles 4
- 4(3). Apical corial margin straight; hind wing with Sc and lacking intervannals; often brightly coloured with red, yellow, orange and black (Plate 3, V, W) LYGAEINAE
 Apical corial margin sinuate on mesal half; hind wing lacking Sc, with intervannals present; dull brownish yellow, with wings often hyaline (Fig.

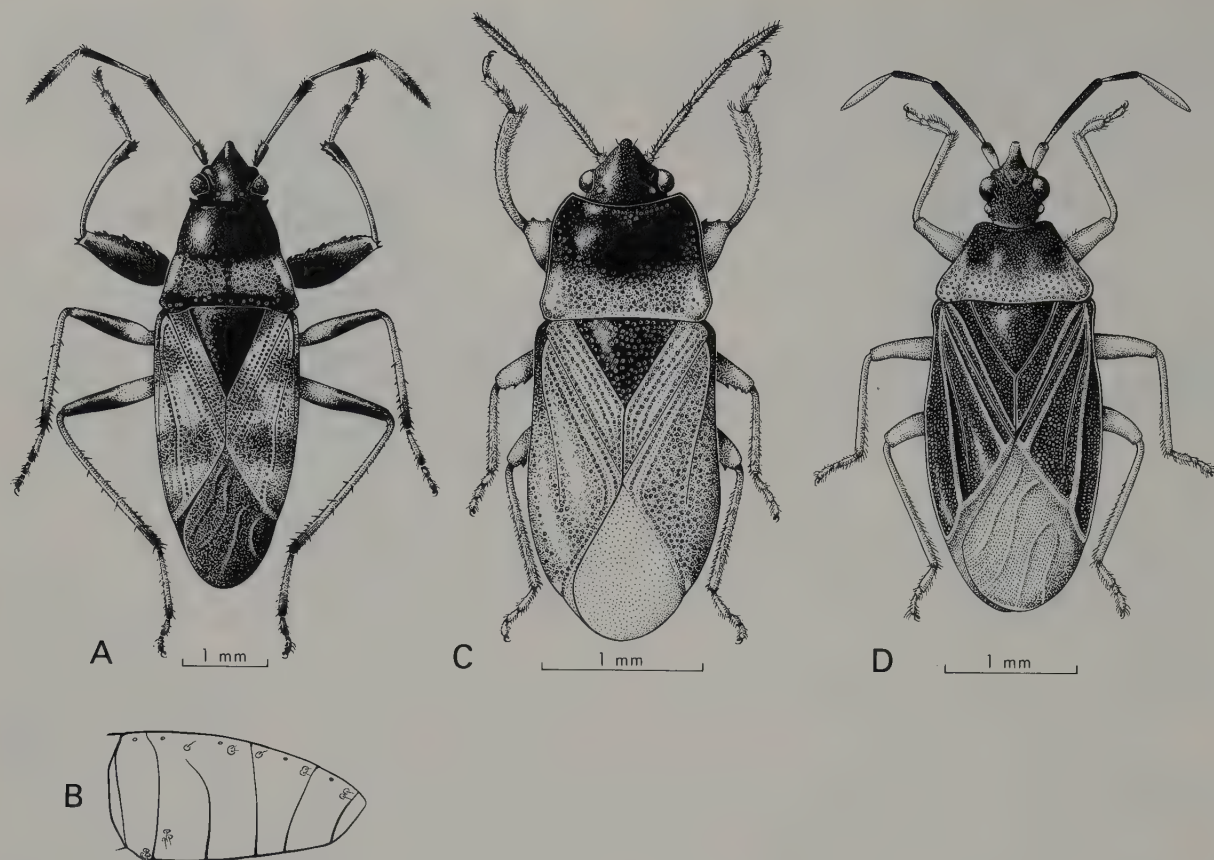


Fig. 30.70 Lygaeidae-Rhyparochrominae: A, *Euander lacertosus*; B, abdomen of same, lateral; C, *Plinthisus* sp.; D, *Clerada* sp.

[T. Nolan]

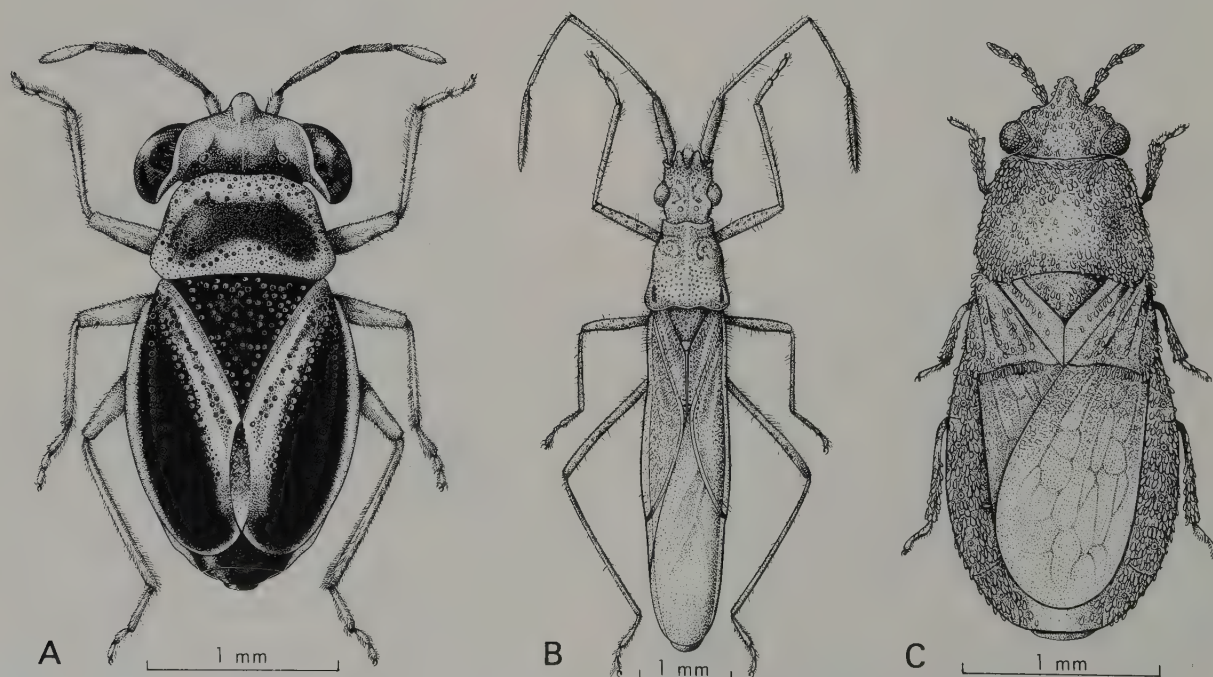


Fig. 30.71 Lygaeidae: A, *Germalus elegantulus*, Geocorinae; B, *Ontiscus* sp., Cyminae; C, *Slaterellus hackeri*, Blissinae.

[T. Nolan]

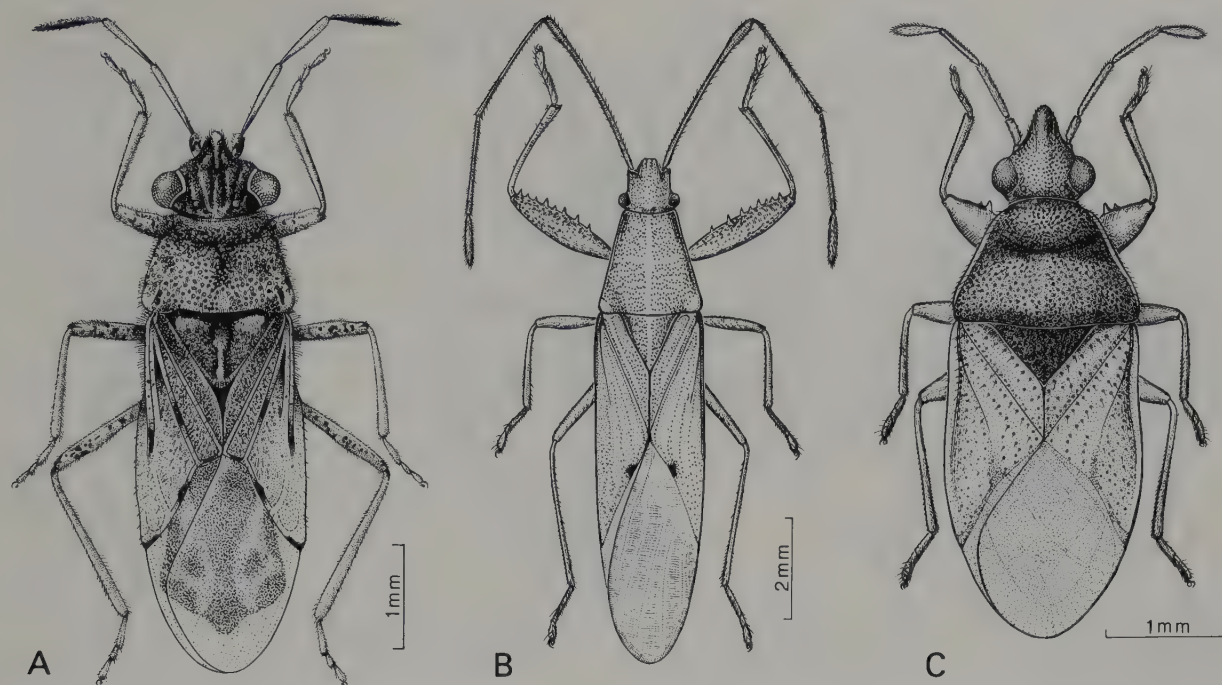


Fig. 30.72 Lygaeidae: A, *Nysius clevelandensis*, Orsillinae; B, *Pachygrontha austrina*, Pachygronthinae; C, *Cromptus opacus*, Ischnorhynchinae.

[A by T. Nolan; B,C by S. Monteith]

- 30.72A) ORSILLINAE
- 5(2). Spiracles of abdominal segment 7 located ventrally, all others dorsal 6
- With at least spiracles of abdominal segments 6 and 7 located ventrally 8
- 6(5). Hemelytra impunctate or at most with weak, scattered punctures [Fig. 30.71c] BLISSINAE
- Hemelytra coarsely punctate 7
- 7(6). Bucculae short, not extending caudad of base of antenniferous tubercles; trichobothria present laterally on S3–7 [Fig. 30.71b] CYMINAE
- Bucculae elongate, extending to base of head; trichobothria present laterally only on S5 and S6 CRYPTORHAMPHINAE
- 8(5). Spiracles on abdominal segments 3 and 4 placed dorsally 9
- Spiracles on abdominal segments 3–7 placed ventrally 10
- 9(8). S2–4 with sutures fused and obliterated; without lateral trichobothria on these segments; ant-mimetic BLEDIONOTINAE
- S2–4 with sutures present and with lateral trichobothria; body generally short and stout, not ant-mimetic (Fig. 30.71a) GEOCORINAE
- 10(8). S3 and S4 lacking lateral trichobothria HENICOCORINAE
- S3 and S4 each with 2 or 3 lateral trichobothria 11
- 11(10). Spiracles of abdominal segment 2 placed dorsally 12
- Spiracles of abdominal segment 2 placed ventrally 13
- 12(11). Lateral pronotal margins explanate or laminate (Fig. 30.73a) ARTHENEINAE

Lateral pronotal margins rounded or at most slightly carinate, never conspicuously explanate

..... OXYCARENINAE

- 13(11). A cross-vein present in membrane of fore wing creating a closed basal cell; fore femora at most weakly incrassate and with few spines; hamus of hind wing arising distad of point on discal cell where Cu diverges as a free vein

..... HETEROGASTRINAE

Neither cross-vein nor closed cell basally in membrane of fore wing; fore femora strongly incrassate and heavily spinose; hamus of hind wing arising in discal cell basad of divergence of Cu as a free vein (Fig. 30.72b) PACHYGRONTHINAE

The RHYPAROCHROMINAE are the dominant subfamily with over 100 species in Australia (Fig. 30.70). Most feed on ripe seeds that have dropped to the ground (J. A. Slater 1976). Flightlessness is common and results in many different modifications of the fore wing (coleoptery, brachyptery, microptery etc.; J. A. Slater 1975). Several are ant mimics.

The Bassian subregion is dominated by Udeocorini which include *Euander lacertosus*, a widespread species that attacks strawberries. Targaremini are found chiefly in mesic environments in eastern Australia and nearby Pacific islands, with extensive radiation in New Zealand. The Myodochini is a large tribe (24 spp., 13 genera) with most species in Australia confined to northern areas; common species are *Pseudopachybrachius guttus*, *Horridipamera nietneri*, *Remaudiereana nigriceps* and *Paromius gracilis* (Malipatil 1978). Drymini are well rep-

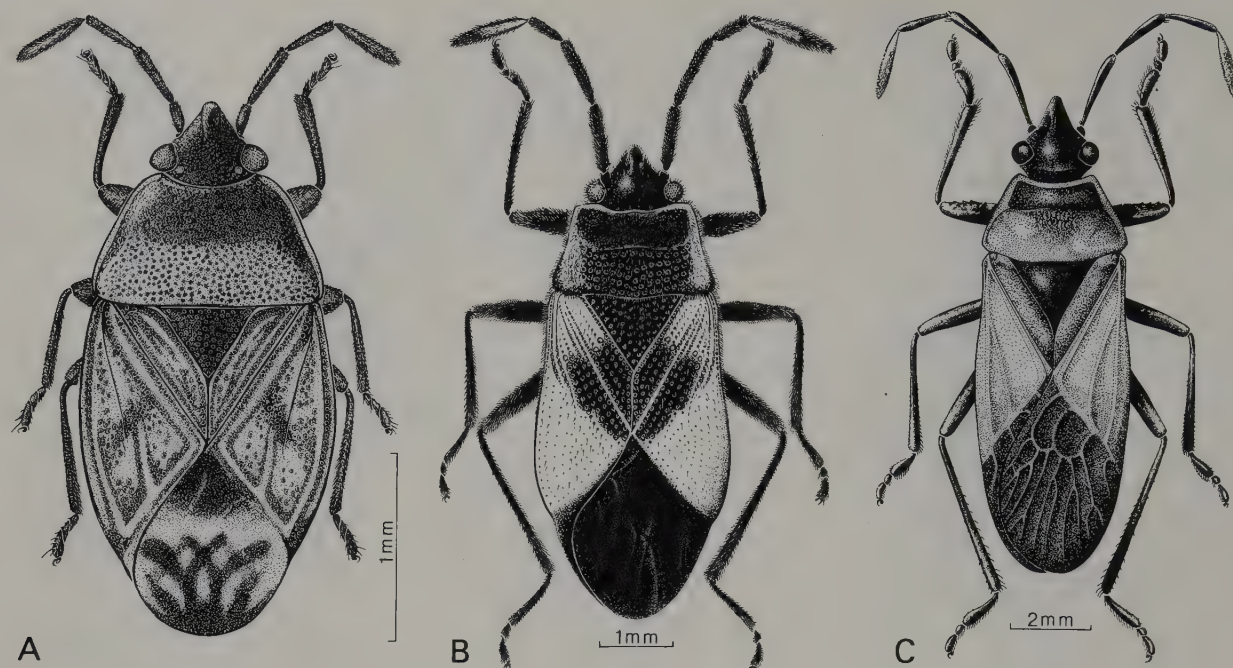


Fig. 30.73 A, *Dilompus robustus*, Artheneinae-Lygaeidae; B, *Delacampius lateralis*, Largidae; C, *Dindymus versicolor*, Pyrrhocoridae.

[A by S. Monteith; B, C by T. Nolan]

resented with 6 of the 10 genera endemic; *Brentiscerus putoni* is common in leaf litter (Gross 1965). Lethaeini include a number of striking, often shining and polished species; there is a flightless, beetle-like endemic group (*Coleocoris* and *Carabocoris*) and a Torresian element with close relationships to the Oriental region. Cleradini are flattened and feed on vertebrate blood; some Australian species feed on the blood of small marsupials (Wilton-Smith 1978). The Australian cleradine fauna is relatively rich with several endemic genera (Malipatil 1983). Rhyparochromini are poorly represented. *Dieuches* (14 spp.) comprises most of the fauna (Eyles 1973). Plinthisini include 15 small to minute species of *Plinthisus*; most are Bassian and flightless with staphylinoid fore wings (Slater and Sweet 1977). Lilliputocorini are minute and yellowish brown, and inhabit forest litter in all major tropical areas, including north-eastern Australia (Slater and Woodward 1982).

The Australian LYGAEINAE (Plate 3, V, W; Fig. 2.40; 63 spp., 13 genera) are mostly large and brightly coloured, with red and black predominating. *Oncopeltus sordidus* is a minor pest of cotton and *Graptostethus servus* has been taken on various crops in northern regions, including W.A. [A. Slater 1985]

ORSILLINAE (Fig. 30.72A) are much smaller and grey, with almost transparent wings. *Nysius vinitor*, the Rutherglen bug, is ubiquitous in Australia and often occurs in swarms in dry pastures. It attacks a variety of crop and garden plants.

CYMINAE (Fig. 30.71B) are small, brown bugs that live in seed heads and resemble seeds of various sedges and rushes. *Ontiscus* is primarily Australian (Hamid 1975).

CRYPTORHAMPHINAE are also small and brown; *Crypto-*

rhampus occurs in Australia and *Gonystus* in Australia and Fiji (Hamid 1971).

The BLISSINAE, often known as chinch bugs, are unusual in that they feed upon the sap of monocotyledonous plants rather than upon seeds. They occur most commonly on grasses but also on sedges. Most blissines are narrow, parallel-sided and flattened; brachyptery and microptery are common. *Australodemus*, *Heinsius*, *Slaterellus* (Fig. 30.71C) and *Archaeodemus* are endemic (J. A. Slater 1979).

GEOCORINAE (Fig. 30.71A) have broad heads and prominent eyes. Most Australian species belong to the widespread genera *Germalus* and *Geocoris* and are either phytophagous or predacious.

Of the OXYCARENINAE only *Oxycarenus* (4 spp.) is recorded from Australia. Adults are small, with black and white hemelytra, and sometimes occur in large numbers. Nymphs are red. *O. luctuosus* and *O. arctatus* feed on malvaceous plants, including cotton, and also damage fruit, nuts and other crops.

PACHYGRONTHINAE (Fig. 30.72B) are elongate, coarsely punctate and mostly brown or black. The Australian fauna is highly endemic. The pale yellow *Stenophyella macreta* is often common in seed heads of grasses. *Darwinocoris australicus* is usually micropterous and feeds on Restionaceae in W.A. (J. A. Slater 1955, 1976).

ISCHNORHYNCHINAE (Fig. 30.72C; 6 spp.) are small and subovoid, with a covering of short, sericeous hairs (Scudder 1962). They feed on a wide range of dicotyledons, but the only known host records in Australia are of Myrtaceae (*Callistemon*, *Leptospermum*, *Metrosideros*). The most widely distributed species are *Crompus oculatus* and *C. opacus*.

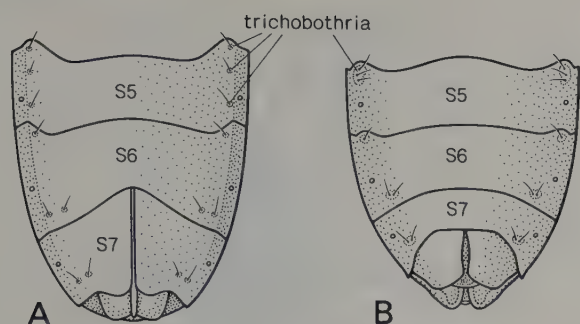


Fig. 30.74 Apex of abdomen of ♀, ventral: A, *Physopelta gutta*, Largidae; B, *Dindymus versicolor*, Pyrrhocoridae. [S. P. Kim, S. Monteith]

Australian HETEROGASTRINAE (5 spp.) may all feed on *Ficus* seeds. *Woodwardothignus gracilis* is an endemic ant mimic from North Qld (J. A. Slater 1981).

ARTHENEINAE (Fig. 30.73A) are represented by *Dilompus* (2 spp.), comprising an endemic tribe (J. A. Slater *et al.* 1962). HENICOCORINAE is an endemic Australian subfamily containing only the broad, flattened, flightless *Henicocoris monteithi* (Woodward 1968a). BLEDIONOTINAE are ant mimics; *Austropamphantus woodwardi* is the only Australian species (J. A. Slater 1981).

84. Largidae (Plate 3, Y; Figs 30.73B, 74A). Largids are phytophagous and resemble pyrrhocorids in general appearance. Australian species belong to *Physopelta* and

Delacampius. *P. gutta* (Plate 3, Y) which is found from Qld to Vic. and the similar-looking *P. australis* from Qld and the N.T. are the commonest species.

85. Pyrrhocoridae (Plate 3, X; Figs 30.73C, 74B). Cotton stainers feed mostly on Malvaceae but are occasionally found on other plants. *Dysdercus cingulatus* and *D. sidae* occur in the northern third of the continent and will attack cotton, staining the lint and damaging the seed. These two species are very similar, both being yellowish brown to orange with a red head and a small black spot on each corium. There are several species of *Dindymus*. *D. versicolor*, the harlequin bug, occurs in Tas., Vic., N.S.W. and S.A. and occasionally damages deciduous fruit. It is red and black dorsally without central corial spots, and the abdomen is green ventrally.

Superfamily COREOIDEA

by G. F. GROSS

Most coreoids have a series of longitudinal accessory veins in the membrane of the fore wings which distinguishes them from lygaeids, and possess ocelli which distinguishes them from largids and pyrrhocorids. Schaefer (1965) studied the morphology and classification of the Rhopalidae, Alydidae and Coreidae but did not consider the Stenocephalidae or Hyocephalidae, both of which are included here. [Kumar 1965, 1966]

Key to the Families of Coreoidea Known in Australia

1. Base of abdomen ventrally with an ovoid, pore-bearing plate on each side (Fig. 30.76B); opening of metapleural scent gland with bristle-like process (Fig. 30.76B) **Hyocephalidae**
Base of abdomen without such plates; opening of metapleural scent gland without bristle-like process 2
- 2(1). Paraclypei acuminate and meeting in front of clypeus; 1st antennal segment shorter than head (Fig. 30.75); S7 cleft in mid line (cf. Fig. 30.74A); ovipositor long and lacinate **Stenocephalidae**
Paraclypei usually neither acuminate nor meeting in front of clypeus (Fig. 30.77), but if they do, then 1st antennal segment longer than head (Fig. 30.78A); S7 not cleft in mid line (cf. Fig. 30.74B); ovipositor short 3
- 3(2). Metapleural scent gland openings with peritremes usually obsolete, but, if visible, each leading into 2 divergent grooves; T5 (4th visible) constricted in mid line; corium often with a large hyaline area (lacking in most Australian species) [Fig. 30.78C] **Rhopalidae**
Metapleural scent gland openings with distinct peritremes; posterior margins of T4 and T5 produced posteriorly in mid line; corium without a large hyaline area 4
- 4(3). Stout, robust species (usually), with relatively thick legs (Fig. 30.77); bucculae extending to, and usually behind, level of antennifers; head usually much less than half as wide as base of pronotum **Coreidae**
Narrow, elongate species with relatively long, slender legs (Figs 30.78A, B); bucculae very short, not extending behind, and rarely reaching level of, antennifers; head more than half as wide as base of pronotum **Alydidae**

86. Stenocephalidae (Fig. 30.75). This family combines lygaeoid and coreoid features (Lansbury 1965–66) and is represented in Australia by *Dicranocephalus*. In other countries Euphorbiaceae are known as hosts.

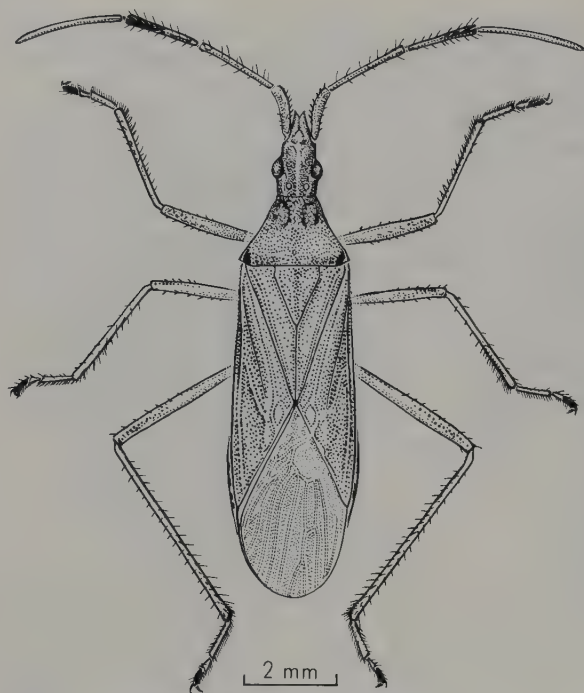
87. Hyocephalidae (Fig. 30.76). A small, endemic family of brown or black species resembling the larger Lygaeidae; some macropterous and some brachypterous; apparently also seed feeders. Štys (1964) studied their morphology and relationships. The recorded species belong to *Hyocephalus* and *Maevius*.

88. Coreidae (Plate 3, Z; Figs 30.7D–F, 10F, 12, 77). Coreids are large-sized bugs with strong repellent odours. Because the New World genus *Anasa* feeds on Cucurbitaceae, they have acquired the name squash bugs. Some

of the Australian species feed on leguminous plants, tending to favour the woody Mimosaceae and Caesalpiniaceae more than the Fabaceae; others feed on eucalypts.

PSEUDOPHLOEINAE lack a longitudinal sulcus on the head, have rounded tibiae and T7 laterally strongly produced. The 4 Australian species belong to *Clavigralloides* and *Gralliclava*. [Dolling 1978]

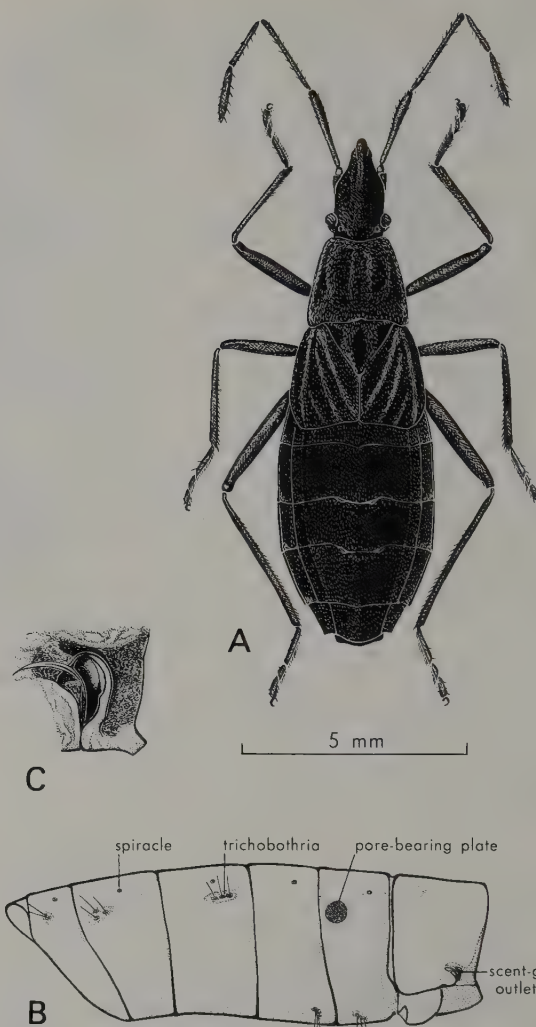
AGRIOPOCORINAE are usually micropterous or apterous but macropters are known. *Agriopocoris* (5 spp.) has a broad abdomen and resembles nymphs of other coreids; some species have been captured on low acacias and other heath-like plants. *Tylocryptus egenus* has a slender abdomen and stick-like appearance, and strongly resembles the *Casuarina* branchlets on which it lives.

Fig. 30.75 *Dicranocephalus* sp., Stenocephalidae.

[S. Monteith]

Of the COREINAE, only *Amorbus* (about 15, very similar-looking spp.) has radiated to any degree in Australia; species are large, robust, brown, have much stouter hind femora in males than in females, and have expanded or spined hind tibiae; they feed on the shoots of eucalypts. *Mictis profana*, the crusader bug, which is widespread in Australia and also from the Moluccas to Fiji, is easily recognised by the yellowish markings forming a cross on the closed hemelytra. Its favoured hosts are *Acacia* and *Cassia* but in Australia it is also a minor pest of citrus. *Leptoglossus gonagra*, originally from the Central American and Caribbean region, is common in northern Australia. It is black with a transverse, red line across the pronotum and the hind femora have large, flattened extensions; it damages cucurbits, pawpaw, passionfruit and citrus. Several species of *Amblypelta* (fruit-spotting bugs) are important pests of a wide range of fruits in northern Australia (Donaldson 1983a). The false cotton stainer, *Aulacosternum nigrorubrum*, is red or brownish red with black membranes and appendages. *Cletus* and the elongate *Pompanotus* and *Turrana* also occur in Australia. [Schaefer 1965]

89. Alydidae (Figs 30.78A, B). Alydids are brown or grey with longish antennae and legs. The Australian fauna has few endemics. Nymphs of some species mimic ants. *Leptocoris acuta*, *L. oratorius* and *Mutusca brevicornis* are slender and about 15 mm long; *L. acuta* and *L. oratorius* are common on grasses, and are pests of rice (Ahmad 1965). In *Noliphus erythrocephalus*, another common species, the abdominal dorsum is red with black connexival bars and the posterior angles of the pronotum are strongly spined. *Riptortus serripes*, the pod-sucking bug, is more robust and feeds on *Acacia* but has become a pest especially of beans; it is dark brown with yellow lateral

Fig. 30.76 A, *Maevius indecorus*, Hyocephalidae; B, same, abdomen; C, same, opening of scent gland. [S. Monteith]

streaks, and has the posterior pronotal angles spined and the hind femora with a row of spines.

90. Rhopalidae (Fig. 30.78c). *Leptocoris* (4 spp., 1 endemic) is yellowish brown to purplish red, elongate ovoid, 9–29 mm long and lacks a large hyaline area in the corium (Gross 1960). *Liorhyssus hyalinus* is a widely distributed, pioneer species but in Australia occurs commonly only in the Lake Eyre region. [Göllner-Scheiding 1983]

Superfamily PENTATOMOIDEA

by G. F. GROSS

The shield or stink bugs have a large, usually triangular but sometimes semi-elliptical scutellum which reaches at least to the apex of the clavus but may cover the whole abdomen. Antennae are usually 5-segmented in adults and 4-segmented in nymphs. There is not yet general agreement on classification, groups which are separated as families by some authors being regarded as subfamilies of Pentatomidae by others. [Kirkaldy 1909; McDonald 1966; Gross 1975a]

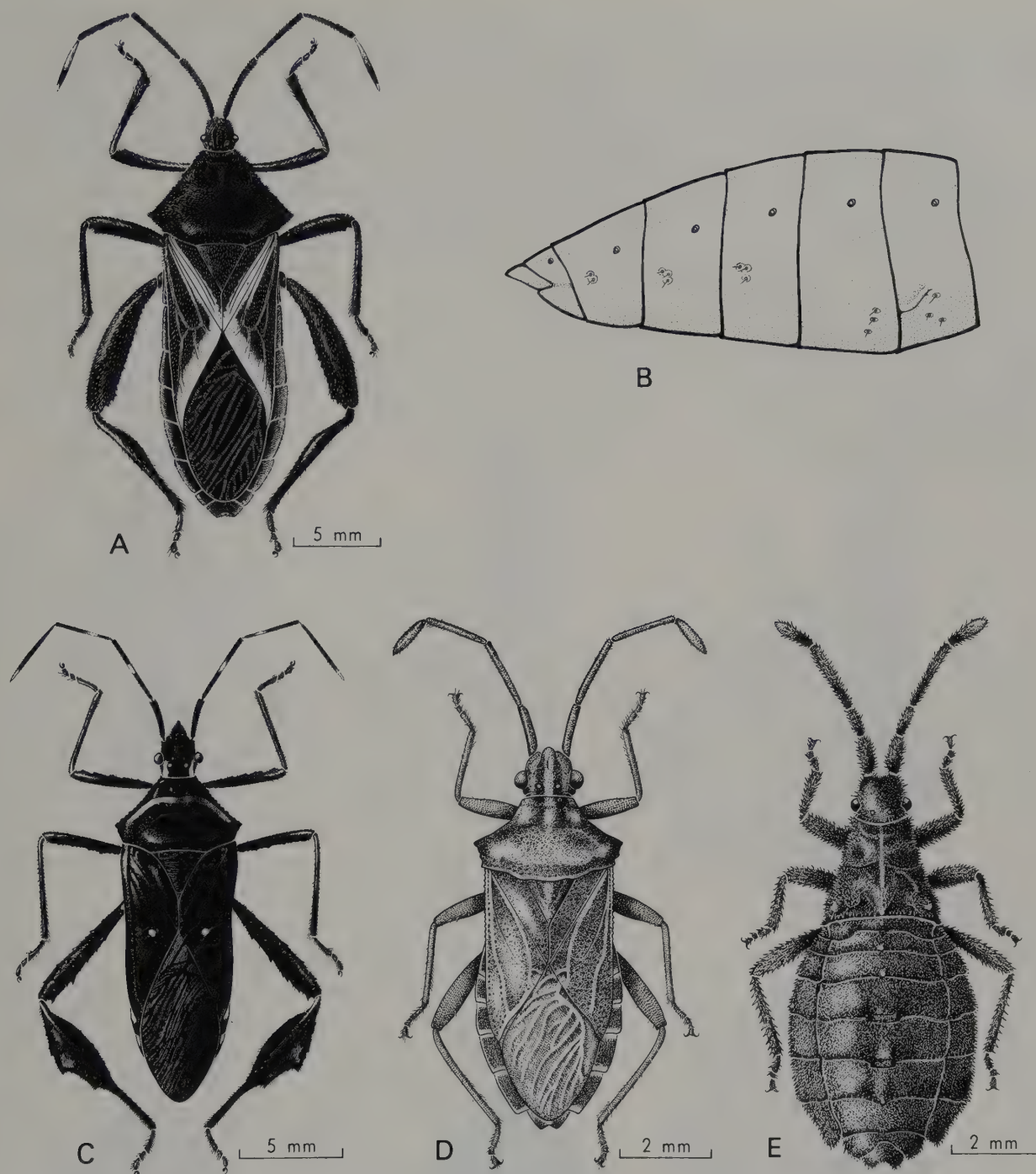


Fig. 30.77 Coreidae: A, *Mictis profana*; B, same, abdomen; C, *Leptoglossus gonagra*; D, *Cletus* sp.; E, *Agriopocoris* sp.

[A, C–E by T. Nolan; B by S. Monteith]

Key to the Families of Pentatomoidea Known in Australia

1. Scutellum very large, convex, more or less U-shaped, completely or almost completely covering abdomen and wings when at rest (Plate 3, P, Q, U; Figs 30.80, 82C) 2
- Scutellum triangular or subtriangular, not covering hemelytra and abdominal region (Plate 3, L–O, R–T; Figs 30.79, 81, 82A, B) 6
- 2(1). Pronotum with large, rounded, posterolateral lobes; meso- and metanotum visible in lateral view beneath base of hemelytron. (Two species of small, convex bugs) **Pentatomidae-APHYLINAE**
- Pronotum without large posterolateral lobes; meso- and metanotum not visible in lateral view 3
- 3(2). Head, pronotum and part of costal margins of hemelytra strongly laminately expanded and recurved to give a tortoise-like appearance (Fig. 30.80B); tarsi 2-segmented **Lestoniidae**

- Head, pronotum and costal margins of hemelytra not strongly laminately expanded and recurved (Plate 3, P, Q, U; Figs 30.80A, 82C); tarsi 3-segmented 4
- 4(3). Hemelytra much longer than abdomen, in resting position folding between corium and membrane to fit under scutellum; abdominal sterna with a straight, black, transverse sulcus on each side; short species often truncate posteriorly and with dorsal surface shining and convex (Fig. 30.80A) **Plataspididae**
- Hemelytra not or scarcely longer than abdomen, not folded between corium and membrane; abdominal sterna without a straight, black, transverse sulcus on each side; form varied but not posteriorly truncate 5
- 5(4). Large and brightly coloured or shining brown species (Plate 3, P, Q, U) but never entirely black, or black with a series of prominent yellow fasciae; if small (*Morbora*) then lateral margins of head, pronotum and anterior half of corium spinose or denticulate; hind wing with a hamus (spur-vein) in the basal cell **Scutelleridae**

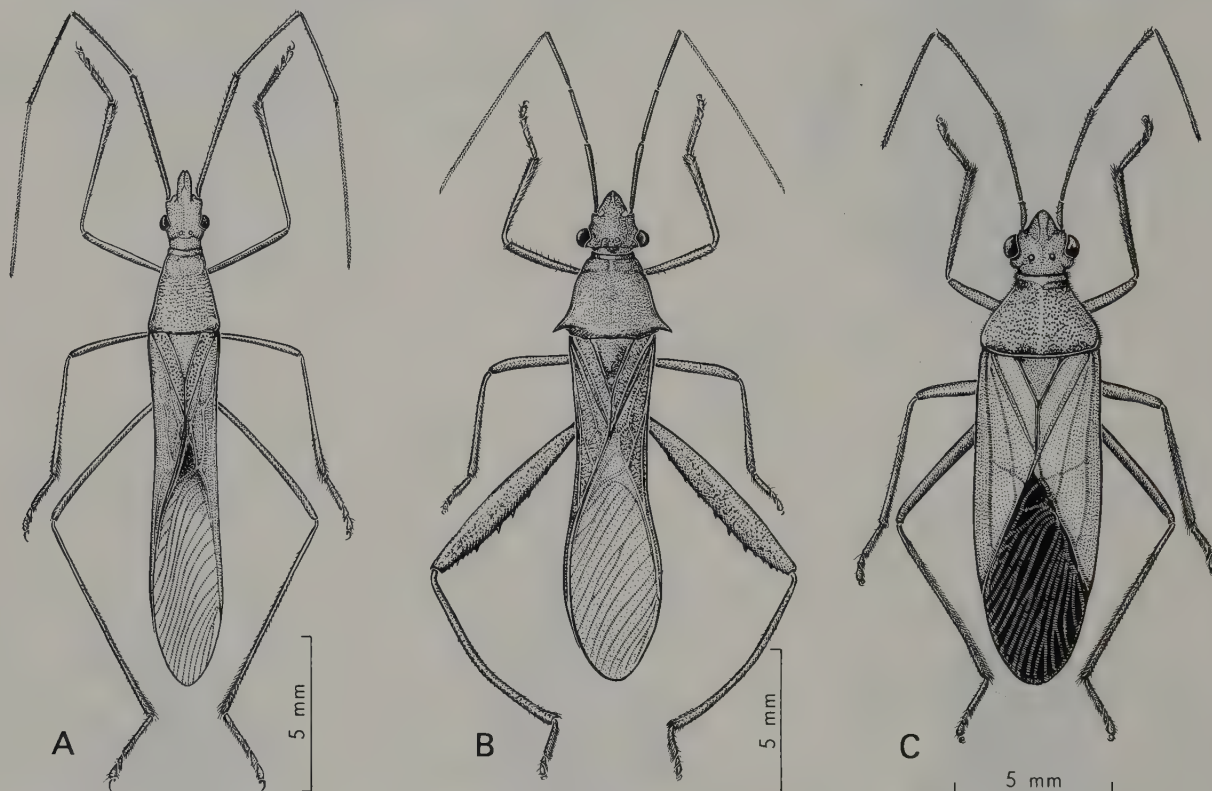


Fig. 30.78 A, *Leptocoris acuta*, Alydidae; B, *Riptortus serripes*, Alydidae; C, *Leptocoris rufomarginata*, Rhopalidae.

[S. Monteith]

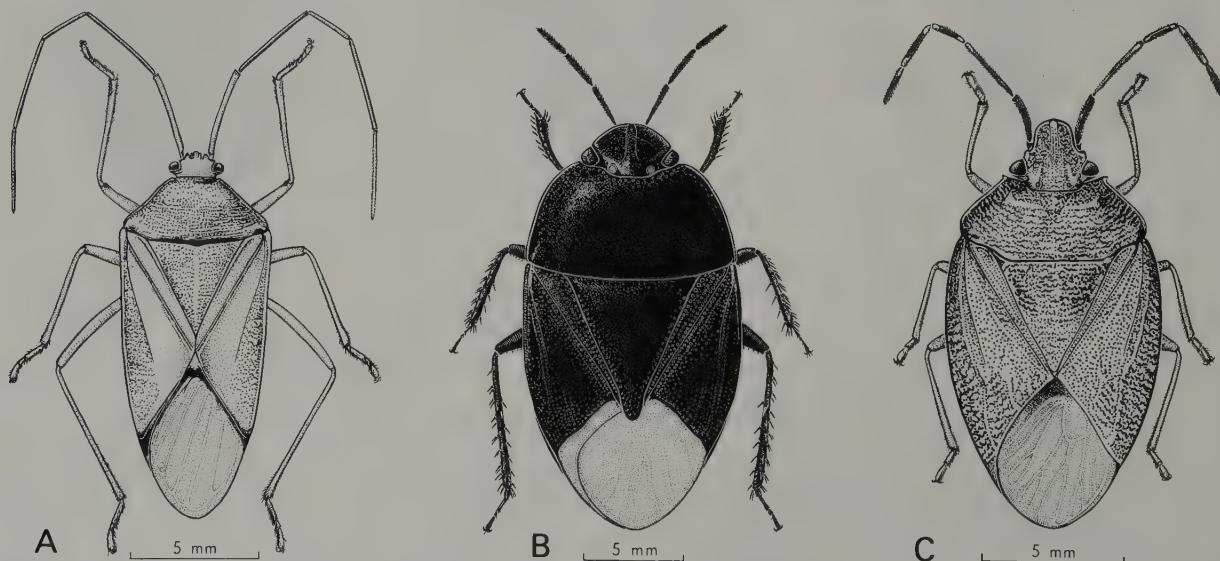


Fig. 30.79 A, *Urolabida* sp., Urostylidae; B, *Adrisa* sp., Cydnidae; C, *Amphaces* sp., Acanthosomatidae.

[S. Monteith]

- Generally smaller and more drab coloured and without spinose or denticulate margins or, if lateral margins of pronotum denticulate or crenulate, then outer margins of head and corium entire; if larger (*Kitsonia*, *Ippatha*), then black or black with yellow stripes; basal cell of hind wing without a hamus **Pentatomidae** (pt)
- 6(1). Tibiae with numerous strong spines (Fig. 30.79B); apices of mid and hind coxae fringed with closely set, rigid setae. [Ovoid, black or brown bugs] **Cydnidae**
- Tibiae without numerous strong spines; apices of mid and hind coxae not fringed with closely set, rigid setae 7
- 7(6). Antennifers cylindrical, smooth, set on lateral margins of head, clearly visible from above (Fig. 30.79A); ocelli close together, sometimes vestigial. [Elongate, green coreid-like bugs] **Urostylidae**
- Antennifers not cylindrical, set below lateral margins of head, and not or only apically visible from above; ocelli usually well separated. [Shield-shaped bugs] 8
- 8(7). Spiracles of abdominal segment 2 (1st visible) fully exposed, removed from posterior margins of metapleura 9
- Spiracles of abdominal segment 2 concealed by metapleura (usually entirely hidden, occasionally spiracle or its peritreme partially visible) 10
- 9(8). Membrane of hemelytron reticulately veined (Fig. 30.81B); antennae 4-segmented in Australian species **Dinidoridae**
- Membrane of hemelytron without reticulate venation (Fig. 30.81A); antennae usually 5-segmented (3rd segment very short) but occasionally 4-segmented **Tessaratomidae**
- 10(8). Tarsi 2-segmented (Fig. 30.79C); ♂ with S8 large and exposed **Acanthosomatidae**
- Tarsi usually 3-segmented (Figs 30.81C, 82), rarely 2-segmented; ♂ with S8 small and concealed **Pentatomidae** (pt)

91. Urostylidae (Fig. 30.79A). Urostylids are delicate, greenish and elongate, and superficially resemble coreids. They are exclusively tropical and represented in North Qld by an undescribed species. Kumar (1971) has studied the comparative morphology of the genitalia and alimentary system.

92. Plataspididae (Coptosomatidae, Brachyplatidae; Fig. 30.80A). Convex, usually shining bugs, which occur mainly in the tropical African and Oriental regions. Australian species belong to *Brachyplatys* (2 spp.) and the large genus *Coptosoma* (13 spp.) and are mainly confined to the Torresian region, though one species reaches the Flinders Ranges, S.A. They have been reported to attack cow-peas in Qld. [Jessop 1983]

93. Cydnidae (burrowing bugs; Figs 30.8C, 79B). Shining black or brown bugs burrowing in the soil and feeding on roots, stems or fallen seeds; often attracted in large numbers to light. All Australian species belong to the CYDNINAE, most to *Adrisa* which has 4-segmented antennae. Other genera have 5-segmented antennae. [Dolling 1981]

94. Acanthosomatidae (Plate 3, R; Fig. 30.79C). Usually rather less sclerotised than most other pentatomoids; tarsi 2-segmented. Australian species are small to medium sized. ACANTHOSOMATINAE occur in both Hemispheres and in Australia extend into the tropics and subtropics. DITOMOTARSINAE and BLAUDUSINAE occur only in the Southern Hemisphere. More species occur in the southern moist parts of Australia than in the arid or northern regions, suggesting a Gondwanan origin for the group. Species most frequently encountered belong to *Anischys*, *Stauralia*, *Hiarchas*, *Duadicus*, *Elasmotherus*, *Eupolemus* and *Amphaces*. [Kumar 1974]

95. Lestoniidae (Fig. 30.80B). A family endemic to Australia, with two species, *Lestonia haustorifera* and *L. grossi*. China (1963) suggested that the ventral abdominal discs function in adhering to some smooth surface, such as leaves or bark; adults and nymphs have been collected on the growing tips of native cypress (*Callitris*). McDonald (1969, 1970) discussed their morphology.

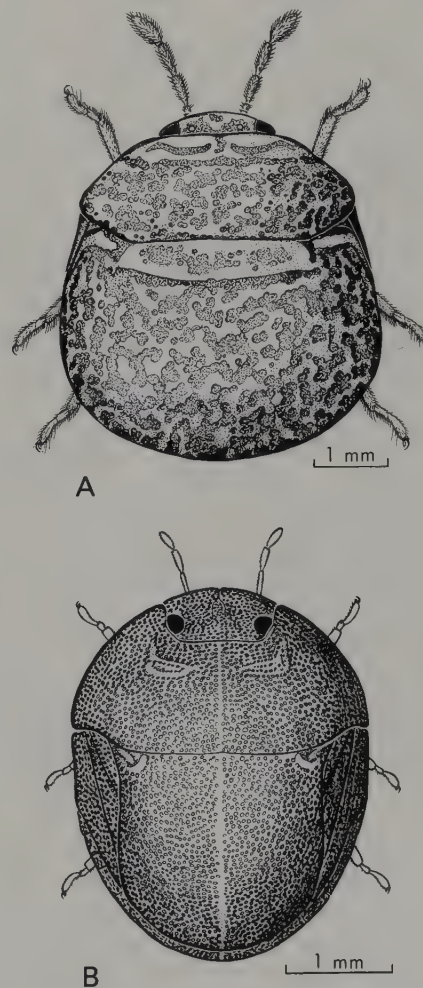


Fig. 30.80 A, *Coptosoma* sp., Plataspididae; B, *Lestonia haustorifera*, Lestoniidae. [S. Monteith]

96. Tessaratomidae (Plate 3, S, T; Fig. 30.81A). The family is essentially tropical and in Australia restricted mostly to the north-east. The bronze orange bug, *Musgraveia sulciventris*, is over 20 mm long, with flattened,

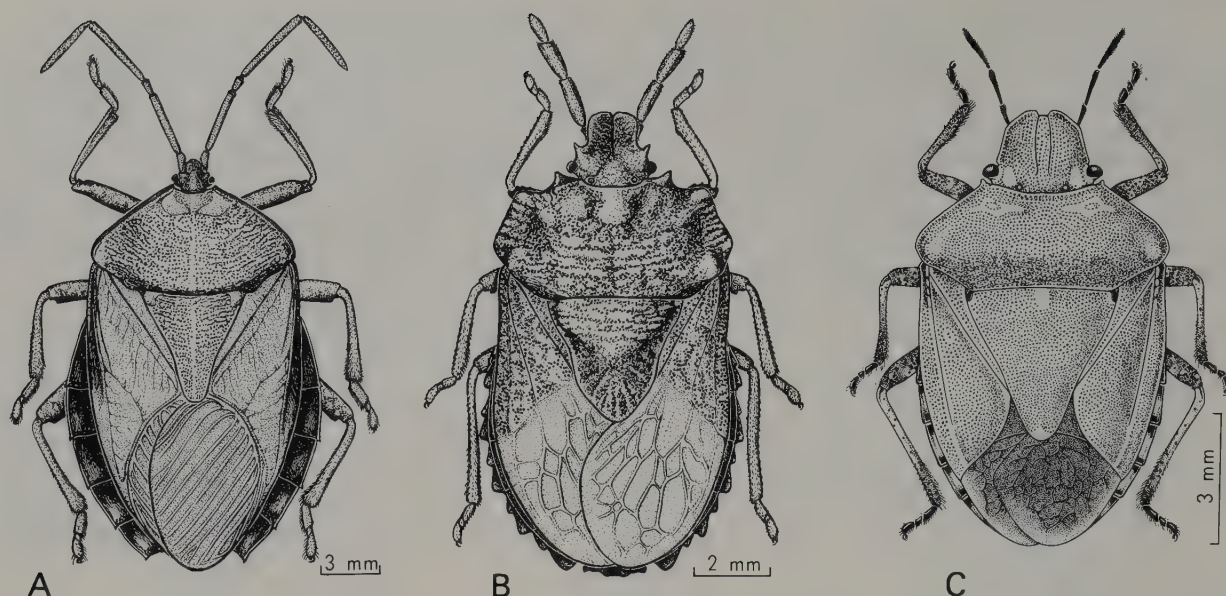


Fig. 30.81 A, *Musgraveia sulciventris*, Tessaratomidae; B, *Megymenum insulare*, Dinidoridae; C, *Dictyotus caenosus*, Pentatomidae.

[S. Monteith; T. Nolan]

ovoid nymphs; its native hosts are Rutaceae and it has become a pest of citrus. *Stilida indecora* is similar in appearance. *Lynamorpha* (2 spp. in eastern Australia) has strongly produced posterior angles to the abdomen. Among Australian Heteroptera *Oncomeris* (2 spp.; Plate 3, S) is surpassed in size only by *Lethocerus* (Belostomatidae). *Erga longitudinalis*, 12–16 mm long, with a pale median band on head, pronotum and scutellum, feeds on the vine *Lonchocarpus blackii*. The most modern subfamily and tribal classification is that of Kumar (1969a, b) based on studies of adults and nymphs. Leston and Scudder (1957) gave a key to Australian genera.

97. Scutelleridae (jewel bugs; Plate 3, P, Q, U; Figs 30.9C, E, 10A, B). Of the ELVISURINAE *Coleotichus*, *Austrotichus* and *Solenotichus* are large and brown. *Coleotichus* occurs in all parts of Australia; *C. costatus* is the most widespread and feeds on *Acacia*. *Morbora* (3 spp.) is the only Australian genus of ODONTOTARSINAE; the species are small, rough, pilose, black and white or brown and white, and widely distributed. The subfamily TECTOCORINAE contains only *Tectocoris diophthalmus* which attacks cotton bolls, and is common on other Malvaceae; known in Qld as the cotton harlequin bug, it occurs in a number of colour forms (e.g. Plate 3, P). Most SCUTELLERINAE are rather elongate, highly coloured and tropical and subtropical. *Choerocoris* (3 spp.) is more stout; *C. paganus*, which feeds on *Dodonaea*, and *C. variegatus* are widespread. *Scutiphora pedicellata* (Plate 3, Q) is found in all the eastern states including Tas. Among the tropical and subtropical species is *Calliphara imperialis*, which is shining orange-red with a metallic green head. *Lampromicra* (Plate 3, U) includes several smaller species, mostly with a ground colour of metallic green or blue. [McDonald and Cassis 1984]

98. Dinidoridae (Fig. 30.81B). Predominantly Oriental

and tropical African, the family is represented in Australia only by *Megymenum insulare* and *M. affine*, which feed on the stems, leaf stalks and young fruit of pumpkins, etc. They are brown to blackish, rugose, not very active species 10–14 mm in length. The record of *Eumenotes obscurus* from Australia has not been confirmed. [Durai 1987]

99. Pentatomidae (shield bugs; Plate 3, L–O; Figs 30.1C, D, 3A, 5D, 6C, F, 7A–C, 8B, 10E, 11B, 81C, 82; 36.7B). Among the Australian Heteroptera the Pentatomidae are second only to the Miridae in number of species. Pentatomids are predominantly brown but may be greenish or highly coloured.

APHYLINAE include only *Aphylum* (2 spp.) which is restricted to southern Australia. Aphyline are mostly found sheltering under *Eucalyptus* bark. They are convex, brownish bugs with an enlarged scutellum and the pronotum deeply excised just lateral to the hemelytral bases. The claspers are made up of two articulated sections but otherwise the male and female genitalia are of the pentatomid type. [McDonald 1966; Gross 1975a]

All other Australian pentatomids belong to the PENTATOMINAE, which can be subdivided into groups of genera (some endemic) based on the structure of the thoracic sternites and genitalia (Gross 1975a, 1976). Genera which have speciated extensively in Australia include *Poecilometis* (39 spp.; Gross 1972), *Cuspicona* (20 spp.; Gross 1975b), *Oncocoris* (20 spp.; McDonald and Edwards 1978), *Cephaloplatus* (16 spp.; Gross 1970), *Ocirrhoe* (11 spp.; Gross 1975b), *Vitellus* (10 spp.) and *Eribotes* (9 spp.). The introduced green vegetable bug, *Nezara viridula*, is a widespread pest in the warmer parts of the world; it feeds on a wide range of vegetable crops, especially beans and tomatoes. *N. viridula* is about 15 mm long and very similar in appearance to the endemic *Glaucias amyoti*, a minor pest of vegetables in Qld. The

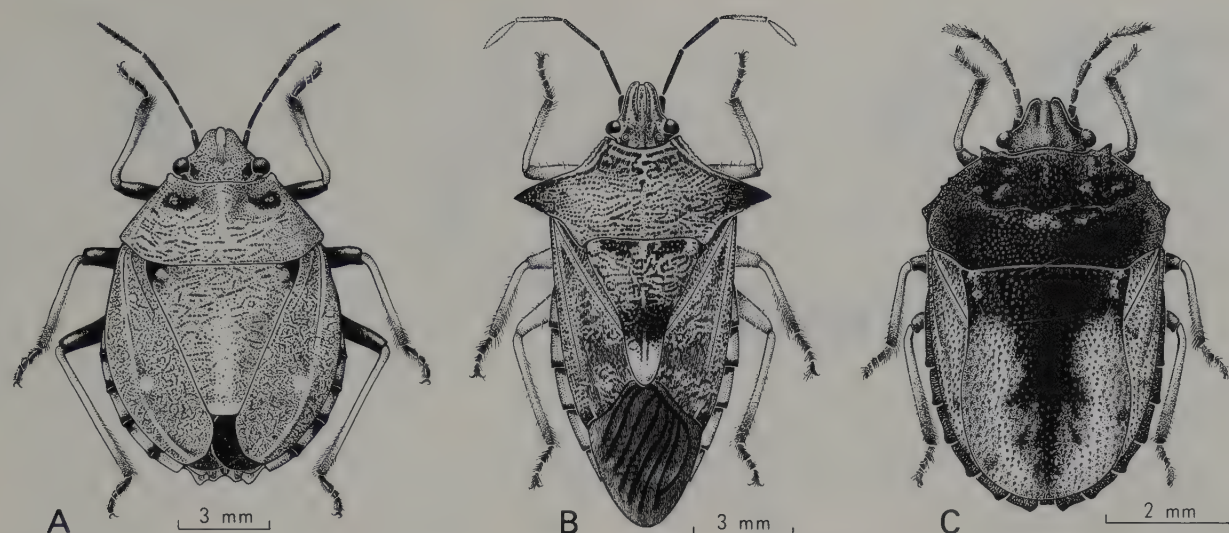


Fig. 30.82 Pentatomidae: A, *Hypogomphus bipunctatus*; B, *Oechalia schellebergii*; C, *Coracanthella geophila*.

[A, B by S. Monteith; C by T. Nolan]

pronotum is strongly punctate in *N. viridula* but almost smooth in *G. amyoti*. *N. viridula* is now partially controlled by the introduced egg parasite, *Trissolcus basalus* (HYMN: Scelionidae). The most colourful, common pentatomine is the horehound bug, *Agonoscelis rutila*, which is up to 12 mm long and conspicuously marked in red and black. The spined citrus bug, *Biprorulus bibax*, is green and about 18 mm long with strong lateral spines on the pronotum; it feeds on citrus and related native Rutaceae in the eastern states and in the Murray Valley. The green potato bug, *Cuspicona simplex*, is also green with spinose pronotal angles; it is related to but smaller than *B. bibax* and a pest of a range of crops. *Poecilometis* spp. (Plate 3, M) are large, brownish or blackish, sometimes greyish, often have strong lateral spines on the pronotum and feed on eucalypts. *Alcaeus* and related genera resemble but are not closely related to *Poecilometis*; they feed on acacias. *Piezodorus hybneri* feeds extensively on *Callitris*. *Andrallus*, *Oechalia*, *Platynopus*, *Amyotea*, *Cermatulus* and *Jalloides* are all predacious. *Cermatulus nasalis*, which feeds on the pear and cherry slug (larva of the sawfly *Caliroa cerasi*—Tenthredinidae), and *Oechalia schellebergii* (Fig. 30.82B) which feeds on the larvae of the grapevine moth, *Phalaenoides glycinae* (Agaristinae)

are the two commonest species in this group. All the species discussed so far in this subfamily have the usual triangular scutellum, but there are a number of groups of genera in Australia characterised by a greatly enlarged scutellum. Some of these groups are endemic, with the most conspicuous being *Ippatha* which is bright yellow with longitudinal, and sometimes transverse, black or brown stripes; it is often mistaken for a scutellerid. *Thryptomenecoris officieri*, from the Great Victoria Desert, is another species with an enlarged scutellum; with a length of about 3.3 mm it is the smallest known pentatomid. [Gross 1975a, 1976]

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Thysanoptera

(Thrips)

L. A. MOUND and B. S. HEMING

Small, slender, dorsoventrally compressed, exopterygote Neoptera, with asymmetric piercing and sucking mouth-parts; tarsi with apical eversible bladders; wings, when present, narrow with reduced venation and fringe of long marginal setae or cilia; cerci absent. Metamorphosis intermediate between incomplete and complete, with two or three quiescent, pre-imaginal instars.

There are about 4500 described species of thrips worldwide but the Australian fauna is not well known (Mound and Houston 1987). They range in body length from 0.5 to 15 mm and can be distinguished from other insects by their asymmetric mouth-parts and, as adults, by their eversible, pretarsal bladders (arolia). Fringed wings, from which the order derives its name, also occur on small insects in several other orders. Modern evidence supports the view that thrips share a common, psocopteroid ancestor with the Hemiptera (Lyal 1985a).

Many aspects of structure, biology and phylogeny are reviewed by Mound *et al.* (1980). T. Lewis (1973) reviewed the ecological and economic information. Jacot-Guillarmod (1970–79) and Jacot-Guillarmod and Brothers (1986) catalogued many species.

Anatomy of Adult

Head (Figs 31.1, 2). Broad-based, hypognathous or opisthognathous; capsule without sutures, often striated; dorsum of head in males of some *Merothrips* with a large gland (Moritz 1984); tentorium complete or variously reduced to anterior arms (Moritz 1982c). Compound eyes variable, from almost holoptic to only 3 facets in some apterae. Three ocelli usually present in macropterae. Antennae with 4–9 moniliform to filiform segments, several bearing chemosensory pegs or areas; pedicel with a complex Johnston's organ (Bode 1986). Mouth-parts

arranged as a ventrally-directed cone formed by the labrum, labium and maxillary stipites, and containing paired maxillary stylets (laciniae) and the left mandibular stylet (Moritz 1982a). Maxillary palps 2–8-segmented; labial palps 1–4-segmented.

Thorax. Pronotum conspicuous, with regular pattern of long setae. Pterothorax shorter and broader in apterae than in macropterae. Meso- and metathoracic spiracles present (Mickoleit 1961).

Legs (Fig. 31.1c). Fore legs usually slender, sometimes modified for gripping with large tarsal teeth and swollen femora. Hind legs sometimes folded under body for jumping. Tarsi 1–2-segmented, with an eversible, pretarsal, adhesive arolium (Heming 1971).

Wings (Fig. 31.5). Slender; in Terebrantia with 3 longitudinal veins and marginal fringe of long, socketed setae; in Tubulifera without veins and with fringe cilia not socketed (Ellington 1980). The fore wing scale bears a pair of stout terminal setae which couple with curved setae on the hind wing costa. The wings lie parallel on the abdomen when at rest in Terebrantia but overlap in Tubulifera.

Abdomen (Figs 31.3, 5). Eleven-segmented; in Terebrantia segment 10 usually conical and invaginated ventrally as part of the ovipositor sheath; in Tubulifera drawn out into a conspicuous tube. Spiracles present on segments 1 and 8. Males frequently with glandular areas on

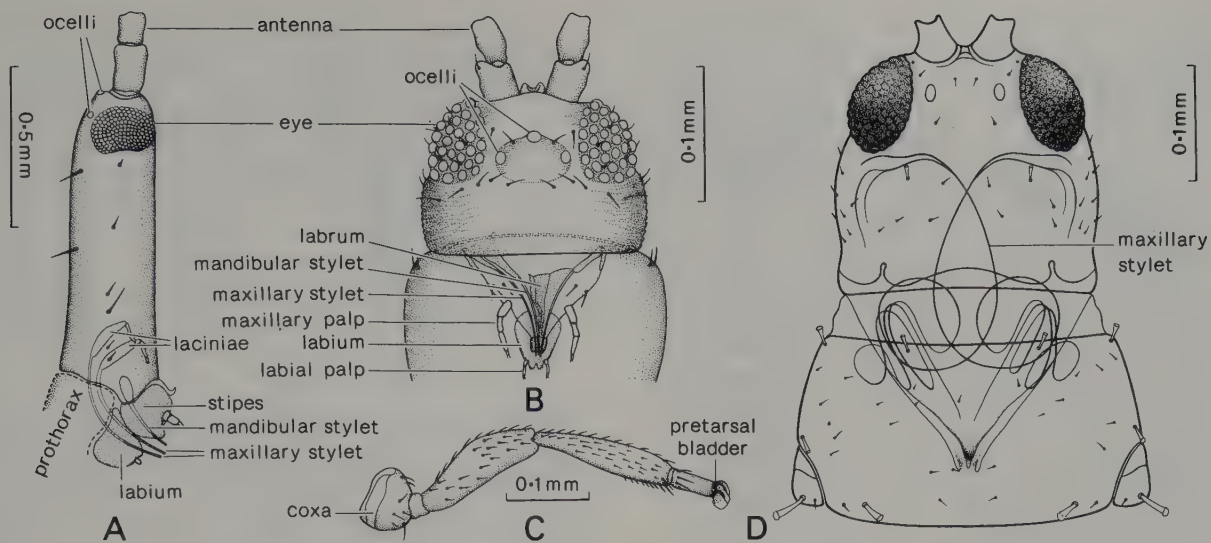


Fig. 31.1 A, head and mouth-parts of *Idolothrips spectrum*, Phlaeothripidae, lateral; B, head of *Thrips australis*, Thripidae, dorsal, with mouth-parts seen through prothorax; C, hind leg of *T. australis*; D, head of *Adrothrips intermedius*, Phlaeothripidae, showing convoluted maxillary stylets. [B. Rankin]

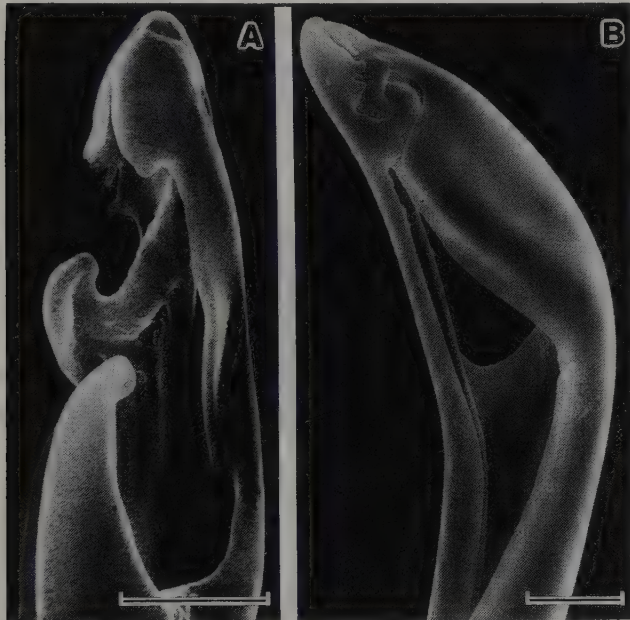


Fig. 31.2 A, *Idolothrips spectrum*, Phlaeothripidae, apex of left maxillary stylet—the feeding aperture is the large opening in the lower foreground; B, *Dinothrips sumatrensis*, Phlaeothripidae, apex of maxillary stylets of larva—right-hand stylet partly flexed with longitudinal tongue and groove detached, feeding aperture in central background, hook-shaped subapical lobe on left stylet corresponds to lobe at extreme left in A. Scale = 10 μ m. [B. R. Pitkin]

one or more abdominal sternites (Bode 1978). Male gonopore between S9 and S10; external genitalia concealed when not in use, symmetrical, with 1 or 2 pairs of parameres, and an eversible endotheca with a more or less sclerotised apex (*pseudovirga*) (Heming 1970b). Females of Terebrantia with gonopore between S8 and S9, and 2 pairs of valves forming a serrated ovipositor (Moritz 1982b) which is reduced in a few thripids and merothripids. Females of Tubulifera with gonopore

between S8 and S9; ovipositor reduced to an eversible chute-like structure (Heming 1970a); internally at the base of T10 these females have a characteristic linear structure (*fustis*) which is a median thickening in the roof of the vagina (Fig. 31.3).

Internal Anatomy. The alimentary canal has a cibarial pump, 2 pairs of salivary glands, an extensive mid gut, 4 Malpighian tubules, and usually 4 rectal papillae of unusual structure (Bode 1977). The nervous system is concentrated, the suboesophageal and prothoracic ganglia being fused, and the abdominal ganglia concentrated in segment 1 (Staub 1979). The male has a pair of fusiform testes and 1 or 2 pairs of large accessory glands. In the female each ovary consists of 4 panoistic ovarioles.

Immature Stages

Egg. Relatively large; operculum present in some Terebrantia together with hatching spines on embryonic cuticle (Kirk 1985b), absent in Tubulifera. Embryogenesis, described only for non-Australian species (Heming 1979; Haga 1985), resembles that of Psocoptera and Hemiptera. A rudiment of the right mandible forms but degenerates during embryogenesis prior to katatrepsis (Heming 1980).

Juveniles (Fig. 31.4). Postembryogenesis closely resembles that of male Coccoidea. Metamorphosis is unusual with 2 (Terebrantia) or 3 (Tubulifera) quiescent 'pupal' stages (instars III to IV or V), in which antennal segmentation is reduced or absent, the mouth-parts are non-functional and the abdominal spiracles are reduced or absent. In addition, significant tissue reconstruction occurs (e.g. in gut, nervous system, body and head musculature). *Caliothrips indicus* pupae in India can imbibe liquid from leaf surfaces, the cibarial pump remaining functional but not the stylets (T. H. Wilson 1975). Instar III has been termed propupa or prepupa (Heming 1970a); in Terebrantia wing rudiments appear in this instar but in instar IV in Tubulifera (Heming 1991). Although these

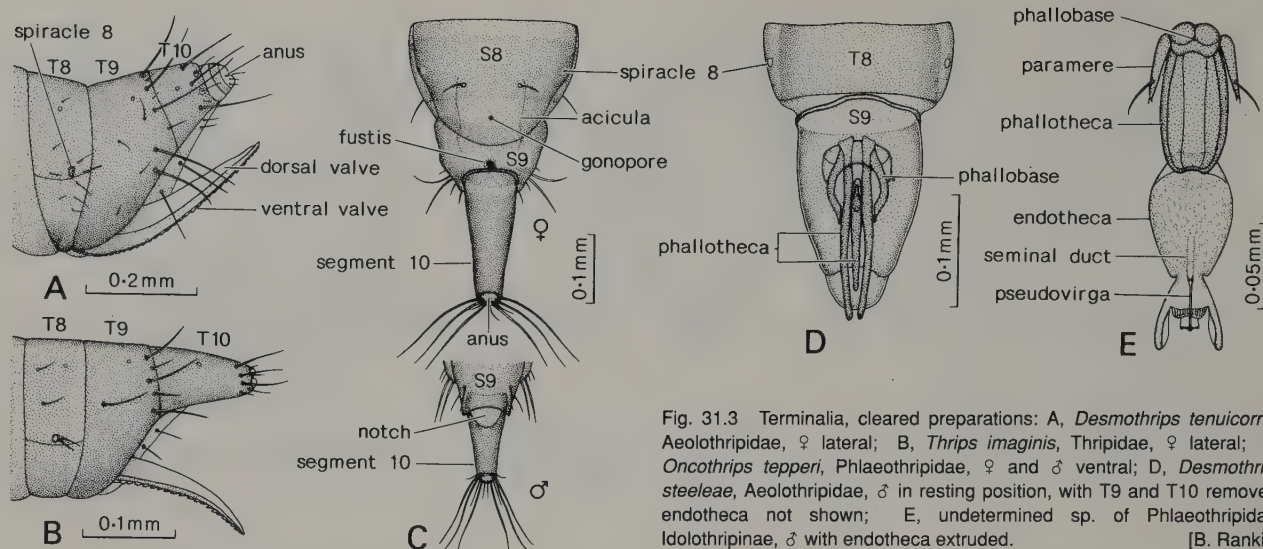


Fig. 31.3 Terminalia, cleared preparations: A, *Desmothrips tenuicornis*, Aeolothripidae, ♀ lateral; B, *Thrips imuginis*, Thripidae, ♀ lateral; C, *Oncothrips tepperi*, Phlaeothripidae, ♀ and ♂ ventral; D, *Desmothrips steeleae*, Aeolothripidae, ♂ in resting position, with T9 and T10 removed, endotheca not shown; E, undetermined sp. of Phlaeothripidae-Idolothripinae, ♂ with endotheca extruded. [B. Rankin]

'pupal' stages have evolved independently of the endopterygote pupa, the term larva is preferred to nymph for instars I and II. The latter resemble wingless adults but with transparent cuticle (Tubulifera often have red or purple internal pigment), antennae 5–7-segmented, compound eyes reduced to 4 (Terebrantia) or 3 (Tubulifera) ommatidia and dorsal ocelli absent.

Prior to ecdysis instar II larvae of various Terebrantia spin a cocoon from silk probably from a gland in the end of the abdomen. Complete metamorphosis in thrips probably arose as larvae specialised for an increasingly sedentary or cryptic life-style.

Biology

Food and Feeding. Thrips presumably evolved from fungus- or detritus-feeding ancestors (Mound *et al.* 1980) and this habit is retained by members of the Merothrip-

idae which are structurally the most primitive Thysanoptera. Feeding on higher plants probably evolved several times. Mosses and ferns are used by few species. Reversion to fungus-feeding has occurred in several evolutionary lines of Phlaeothripidae, most feeding on hyphae but some (Idolothripinae) ingesting spores. Despite the range of food (leaf and flower tissue, pollen, fungi and small arthropods) the feeding stylets are uniform in structure differing mainly in stylet length and diameter. In leaf- and pollen-feeding species (Heming 1978; Chisholm and Lewis 1984; Kirk 1984b) the mandibular stylet punches a hole through which the paired maxillary stylets are inserted. The stylets together form a feeding tube with a sub-terminal opening (Fig. 31.2), and the cibarial pump sucks food through this tube. After feeding thrips often produce a droplet of excreta which dries to a characteristic spot on the host

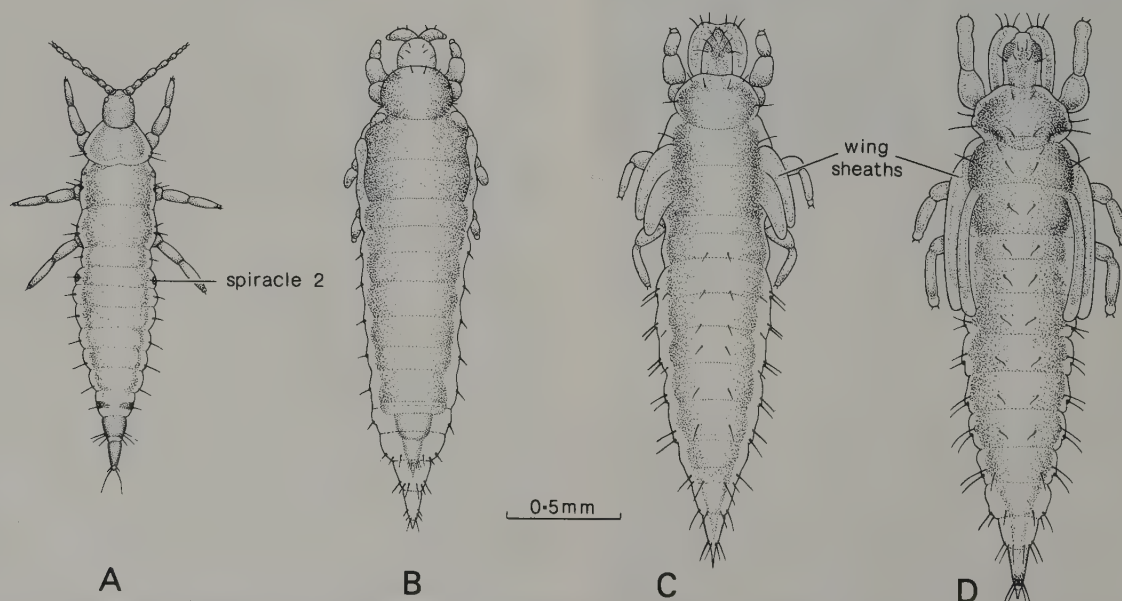


Fig. 31.4 Immature stages of Tubulifera (A, C, D *Teuchothrips* sp., B unidentified): A, larva II; B, 'propupa'; C, pupa I; D, pupa II. The anterior abdominal spiracle is on segment 2 in the larva, on segment 1 in the adult. [B. Rankin]

plant. Idolothripines ingest spores whole through a wide-diameter feeding tube; a proventricular, spore-crushing apparatus is present in the large species of the extralimital genera *Elaphrothrips* and *Mecynothrips*, but not in the Australian genus *Idolothrips*.

Reproduction and Life Histories. Although typically bisexual, most thrips probably reproduce by haplodiploid (arrhenotokous) parthenogenesis. A few species are thelytokous with males rare or unknown (Mound 1976). Male meiosis appears to comprise a single functional mitotic division associated with production of normal and degenerate spermatids; spermiogenesis is aberrant and the mature spermatozoa are unique among insects (Bode 1983). Eggs usually mature one at a time, females of some large species being viviparous or ovoviviparous. Aeolothripids and thripids usually insert each egg into their host plant tissue using the saw-like ovipositor. Phlaeothripids glue their eggs to the substrate near the feeding site, usually laterally but sometimes vertically (Ananthakrishnan *et al.* 1983). Larvae are relatively sedentary, but if feeding on short-lived flowers they must move between flowers as these abscise (Kirk 1984a). Pupation usually occurs near the feeding site, except in flower thrips which pupate in the soil. Adults often disperse before the eggs hatch, but in gall and fungus thrips two generations commonly co-exist. Ecological studies on *Thrips imaginis* are summarised by Kirk (1984a), with observations on intrafloral behaviour and its role in pollination.

Polymorphism and Sociality. Apterae and macropterae are the usual forms, and hemimacropterae are rare, although micropterae with wings scarcely longer than wide are common in Phlaeothripidae. Few species have more than two forms, and continuous variation in wing length is exceptional. Wing reduction is more common in males than in females. Apterae usually lack ocelli, and have reduced eyes, a broader than normal pterothorax, and modified chaetotaxy on the abdominal tergites. Males of fungus-feeding species often exhibit allometric growth patterns, major (oedymorous) males having greatly enlarged fore legs and additional tubercles. Crespi (1986) has described male/male combat in such Phlaeothripidae from Europe and North America, and similar behaviour probably occurs in *Idolothrips* and *Mecynothrips*. In gall-forming species females vary in size and allometric growth, but the significance of this is not known. True social behaviour, including interactions between different generations and communal foraging by larvae, has been described for one bark-dwelling species in Panama (Kiester and Strates 1984).

Flight and Dispersal. Winged adults comb their fringe cilia frequently. These cilia are socketed individually in Terebrantia, each socket being '8'-shaped (Ellington 1980). Before take-off, a thrips combs the cilia from the 'parked' position at one end of each socket and at an angle of 15° to the wing axis, and clicks each one into the opposite end of its socket with the cilia at right angles to the wing axis. In phlaeothripids the cilia are non-articulated extensions of the wing membrane. Many thrips are readily distributed aerially, but apterous adults with the

habit of crawling to the top of grasses and twigs seem to be dispersed by winds more readily than many winged species with cryptic habits. Several winged and wingless Australian thrips seem to cross the Tasman Sea to New Zealand on the wind (Mound and Walker 1982, 1986), and Laughlin (1977) estimated that thrips could survive for 24 hours in the air. In warm weather following a cold spell in Britain, populations of up to 2 million *Limothrips cerealium* per million m³ over cereal crops have been measured (T. Lewis 1973), but subsequent host-finding by sight or scent has been little studied (Kirk 1985a).

Natural Enemies. Adults of *Bagnalliella yuccae*, widespread on *Yucca* plants but not yet recorded from Australia, produce an allomone that repels potential predators (Howard *et al.* 1983). Many phlaeothripids lift the tip of the abdomen over the head in a defensive position, and larvae of the thripid *Heliothrips haemorrhoidalis* frequently exude a droplet from the tip of the abdomen when disturbed. Despite these defensive reactions, thrips are taken by a wide range of predators including anthocorid bugs and chloropid flies (Mound and Walker 1986), mites, chrysopid and coniopterygid larvae and aeolothripids (T. Lewis 1973). Wasps of the genus *Spilomena* (Sphecidae) collect thrips and store them as larval food (Mound and Walker 1982). Eulophid wasps, mainly species of *Ceraninus* (= *Thripoctenus*), are listed by T. Lewis (1973) as thrips parasites. Thrips populations are also susceptible to fungal attack, although the most potent natural agent reducing population levels is probably heavy rainfall.

Economic Importance and Gall Formation. The most important thrips pests in Australia are *Thrips imaginis* on fruit trees, particularly apples, and *Thrips tabaci* on cotton, onions and cucurbits. *Frankliniella schultzei* is an important vector of tomato spotted wilt virus, a disease also carried by *T. tabaci* (Mound 1973). *Thrips simplex* damages gladiolus flowers, and *Thrips hawaiiensis* damages banana fruit. Kirk (1987) gave a key to the larvae of these species and reviewed their host plants. Several panchaetothripines are minor pests of ornamentals in glasshouses, or of tropical and subtropical shrubs and trees. *Anaphothrips obscurus* may cause linear, rust-like markings on cereal leaves. *Haplothrips niger*, a pest of clover in New Zealand, occurs in Australia but is not common. *Haplothrips victoriensis* can be an important predator of *Tetranychus urticae* on lucerne (Bailey and Caon 1986). Species in several phlaeothripid genera cause leaf galls on shrubs and trees including *Acacia*, *Callistemon*, *Ficus*, *Geijera*, *Melaleuca*, *Myoporum* and *Pittosporum*. Galls are induced by adult feeding: either the margin of a leaf rolls, or the lamina folds at the midrib, or the leaf contorts. On *Acacia*, a phyllode produces a bubble which rapidly develops into a globular or cylindrical pouch, the mouth of which is sealed tightly (Mound 1971); large numbers of thrips occur in these galls but their development has not been studied.

Special Features of the Australian Fauna

Mound and Houston (1987) list 422 species in 141 genera from Australia, but this is probably only about half the

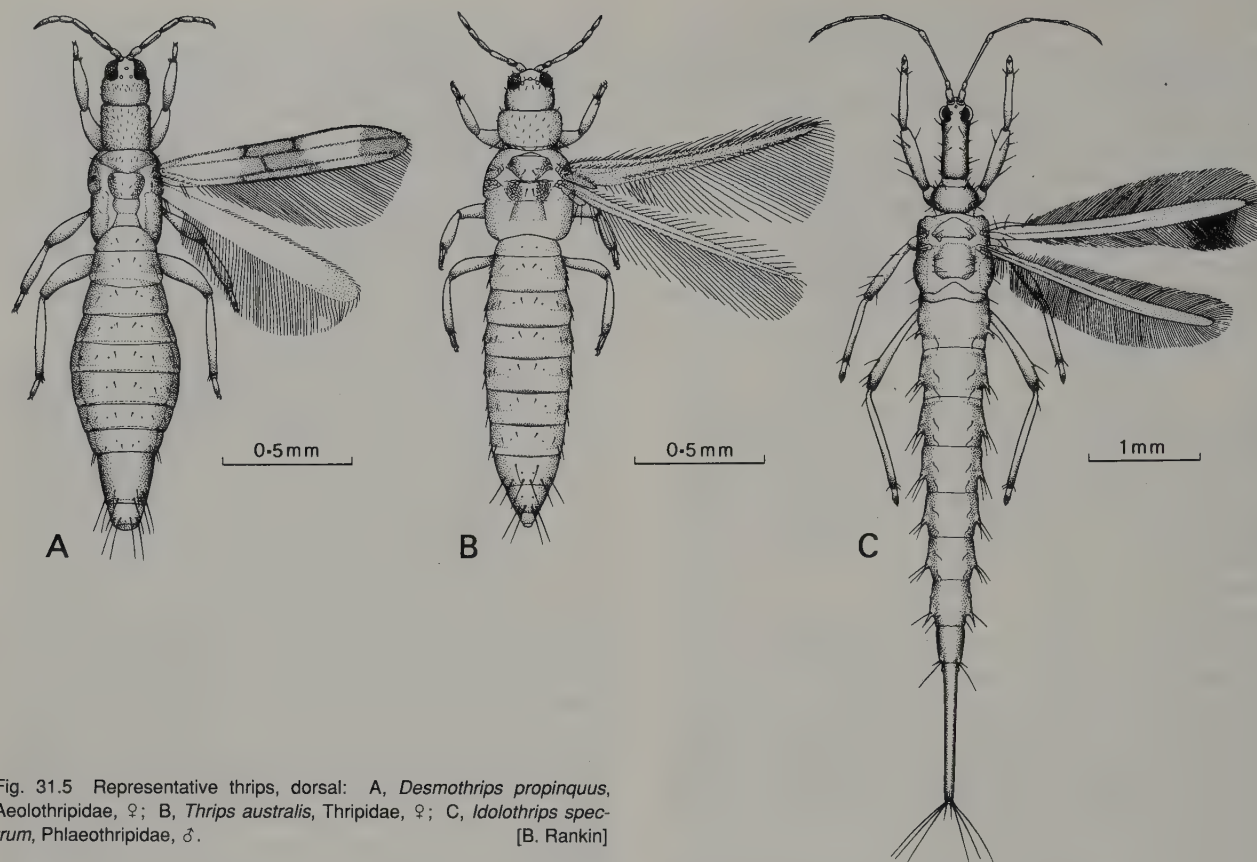


Fig. 31.5 Representative thrips, dorsal: A, *Desmothrips propinquus*, Aeolothripidae, ♀; B, *Thrips australis*, Thripidae, ♀; C, *Idolothrips spectrum*, Phlaeothripidae, ♂. [B. Rankin]

true fauna. The western and inland fauna is almost unknown. The richest fauna seems to be associated with the brigalow country of southern Qld. In the Phlaeothripidae, about 40 of the 89 genera and 240 of the 267 species listed are endemic to Australia; figures for the Aeolothripidae are 3 of 9 genera, and 21 of 24 species, and for the Thripidae about 5 of 42 genera and 65 of 128 species. Many thripid genera have world-wide distributions, but the natural geographical extent of individual

species is often difficult to determine as these insects are so readily distributed by winds and by trade (Mound 1983). The large number of introduced Thripidae probably also results from their small size, protected eggs and frequent polyphagy. A few Australian species have reached New Zealand (Mound and Walker 1982, 1986) and intrusions from the Oriental Region are probably increasing in northern Australia (Mound and Houston 1987).

CLASSIFICATION

Order THYSANOPTERA (422 Australian spp.)

Suborder TEREBRANTIA (155)

1. Merothripidae (3)
- Uzelothripidae (0)

2. Aeolothripidae (24)
- Adiheterothripidae (0)
- Heterothripidae (0)

3. Thripidae (128)
- Fauriellidae (0)

Suborder TUBULIFERA (267)

4. Phlaeothripidae (267)

Eight extant families are currently recognised (Mound *et al.* 1980), but there remains doubt that the two suborders

are sister-groups. Mound and Houston (1987) summarised the distribution and biology of the described fauna.

Key to the Families of Thysanoptera Known in Australia

1. Both sexes with abdominal segment 10 tubular, usually almost cylindrical; wings, when present, without longitudinal veins, wing surface lacking microtrichia, and marginal cilia not socketed; ovipositor chute-like and eversible TUBULIFERA-**Phlaeothripidae**
Abdominal segment 10 always divided ventrally in ♀; fore wings, when present, with costa and usually two longitudinal veins, surface usually with microtrichia, marginal cilia arising from sockets; ovipositor serrate TEREBRANTIA. 2

- 2(1). T10 with a pair of well-developed trichobothria on posterior margin; S8 of ♀ developed as a pair of overlapping lobes each bearing a pair of setae **Merothripidae**
 T10 without trichobothria, or (rarely) with a vestigial pair; S8 of ♀ not developed 3
- 3(2). Cephalic tentorium with well-developed transverse bridge; antennae 9-segmented; fore wing broad with well-developed cross-veins; ovipositor valves upturned **Aeolothripidae**
 Cephalic tentorium reduced, transverse bridge absent; antennae usually 7–8-segmented, rarely 6- or 9-segmented; fore wing slender with only one cross-vein; ovipositor valves downturned **Thripidae**

1. Merothripidae. These fungus-feeding species, which live in leaf litter and on dead twigs, are regarded as the most primitive of extant Thysanoptera. There are about 15 species world-wide in 3 genera, 2 of which are monobasic. *Merothrips* (3 Australian spp.) is predominantly Neotropical but with several species apparently distributed through the tropics and subtropics by trade.

2. Aeolothripidae (Fig. 31.5A). These large flower-thrips usually have broad banded wings, although *Desmothrips reedi* is a bicoloured, often apterous, ant mimic, living at the base of grasses. Most members of the family probably are facultative predators on other small arthropods and also feed on plant tissue or pollen (Kirk 1984b). *Andrewarthaia* (1 sp.) is found in *Eucalyptus* flowers and the recorded colour variation from dark brown to white may be related to differing levels of predation and herbivory (Mound 1972). The family is predominantly Holarctic although *Dorythrips* (2 W.A. spp.) and *Gelothrips* (1 Indo-Australian sp.) occur also in South America, and *Cranothrips* (7 Australian spp.) is represented also in South Africa.

3. Thripidae (Fig. 31.5B). Species of PANCHAETHRIPINAE usually have dark adults with the body surface conspicuously reticulate. These leaf-feeding thrips include several pests, e.g. *Heliethrips haemorrhoidalis* (the greenhouse thrips) and *Selenothrips rubrocinctus* (the redbanded thrips). *Moundothrips* and *Phibalothrips* are unusual in the subfamily in that they live on grasses, while *Australothrips bicolor* is the only thrips living on *Eucalyptus* leaves. THRIPINAE are diverse in structure and biology. *Odontothripella* from legume and grass flowers, and *Pseudanaphothrips* from many other flowers, are the most characteristic Australian genera, although *Thrips imaginis* (the plague thrips) is the dominant flower-living species with *Thrips australis* (= *Isoneurothrips australis*) dominant in *Eucalyptus* flowers. *Chirothrips* and, in the cooler southern areas, *Limothrips* are common on grasses; both genera are introduced, the former living in florets and the latter often on leaves. *Stenchaetothrips biformis* (= *Chloethrips oryzae*), the oriental rice thrips, is found on grasses in moist habitats in Qld, and the European wingless species

Aptinothrips rufus is abundant on grasses further south. The leaf-living thripine fauna is poorly known; *Anaphothrips* includes native and introduced species, *Chaetanaphothrips* includes two pests on banana and orchid leaves and *Scolothrips* includes one or more introduced predators of leaf mites. A remarkable absence from Australia is *Dendrothrips*, an almost cosmopolitan genus of leaf-feeding species with a large, lyre-shaped, thoracic endofurca associated with jumping. *Ensiferothrips primus*, a dendrothripine with remarkably broad wing-setae, occurs on *Casuarina* in Australia and New Caledonia.

4. Phlaeothripidae (Fig. 31.5C). All species of IDOLOTHRIPINAE feed on fungal spores, and 71 in 20 genera are known from Australia. *Idolothrips* and *Mecynothrips* include some of the largest thrips, and males are sometimes dimorphic. In contrast *Allothrips* are small and live in large numbers in dry sclerophyll leaf litter. There are several endemic genera. PHLAEOTHRIPINAE (195 spp.) feed on a wide range of substances, and probably only one third of the true fauna is known. *Podothrips*, *Aleurodothrips* and *Karnyothrips* are predatory on scale insects, most *Haplothrips* are flower inhabiting, particularly on composites and grasses, and *Lissothrips* feed on mosses. About one third of the genera feed on fungus in leaf litter and dead twigs, including *Baenothrips*, *Hoplothrips* and *Psalidothrips*; species definitions in these groups are equivocal due to complex patterns of variation within and between samples (Mound and Walker 1986). Many species feed on green leaves, including species of *Teuchothrips* which cause distorted leaf galls on a wide range of native shrubs. *Geijera* and phyllodinous *Acacia* support several genera of leaf-galling species and inquilines. The pinnate-leaved species of *Acacia* do not seem to support thrips, apart from *Rhopalothripoides froggatti* which is so small that it breeds inside the nectaries on the leaves. *Casuarina* supports a remarkable fauna; most of the species, in several unrelated genera, have very long, often coiled, maxillary stylets (Fig. 31.1D), apparently to reach the chlorenchymatous tissue of these plants which is protected by thick sclerenchyma.

Megaloptera

(Alderflies, dobsonflies)

G. THEISCHINGER

Mandibulate, endopterygote Neoptera, with two pairs of subequal, functional membranous wings and very soft abdomen. Larvae aquatic; mandibulate, with large prothorax, functional legs and lateral abdominal gills. Pupae dectitious and exarate.

The order Megaloptera is supposedly the sister group of the Raphidioptera and is often considered to be the most primitive group of endopterygote insects. About 300 species have been described. The order is widely distributed and diverse through temperate regions, with fewer species in the tropics.

The wing-span of adults ranges from less than 20 mm to 175 mm. They resemble some broad-winged lacewings (Neuroptera) but in Megaloptera there is generally much less end-twigging of longitudinal veins and the abdomen is more soft and very flexible. The aquatic larvae of Megaloptera are recognisable from those of Neuroptera by not having the mouth-parts modified into a sucking tube and by having lateral abdominal gills. Superficially, Megaloptera larvae are also very similar to the larvae of some Gyrinidae (Coleoptera). The labrum and clypeus are distinct in Megaloptera larvae, whereas only a single sclerite is discernible in gyrid larvae.

Van der Weele's (1910) treatment of the world fauna is now outdated but Tillyard (1919a), Riek (1954d), Theischinger (1983) and Theischinger and Houston (1988) have provided comprehensive accounts of the Australian fauna. Theischinger and Houston (1988) catalogued the Australian species.

Anatomy of Adult

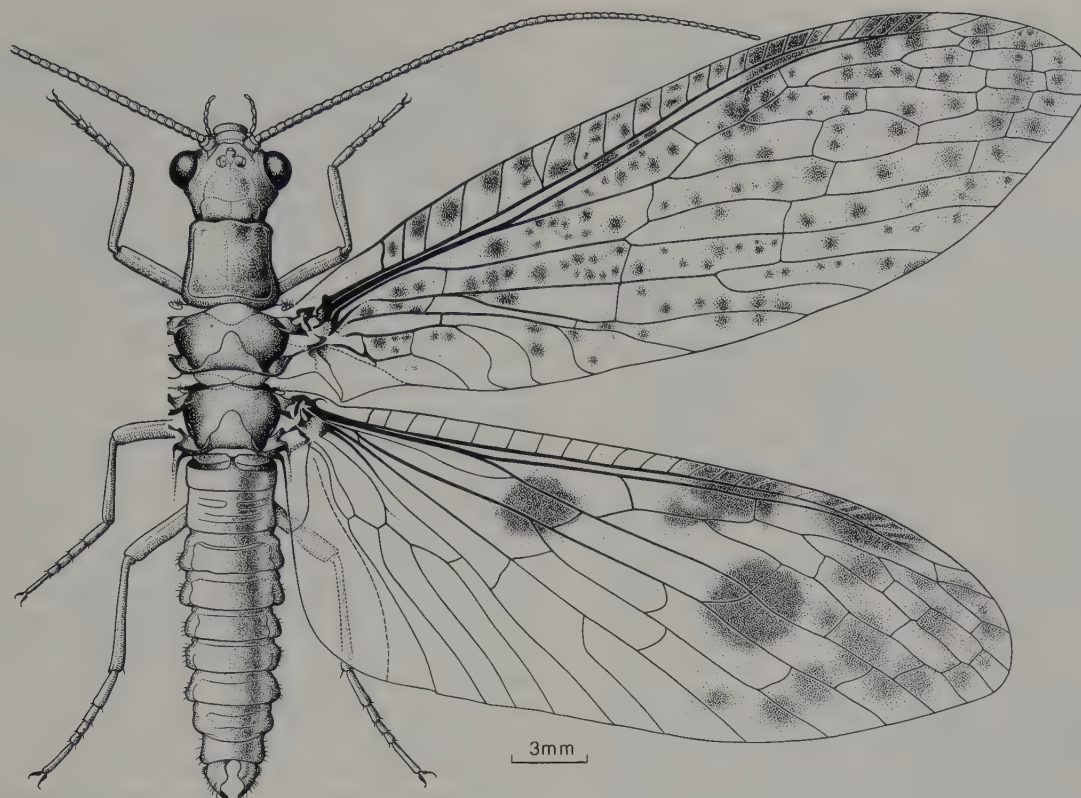
Head (Fig. 32.2). Broad and generally flat, prognathous; compound eyes protruding laterally; postocular sec-

tion large but not prominent in Australian species, expanded and with a spine in some non-Australian taxa. Three ocelli present in Corydalidae; ocelli absent in Sialidae. Antennae slender, multisegmented, filiform or moniliform in all Australian species, serrate or pectinate in males of some non-Australian Corydalidae. Mouth-parts of the biting type, unspecialised; mandibles strong, enormously elongate in males of some non-Australian Corydalidae; maxillary palps usually 5-, rarely 4-segmented; labial palps 3-4-segmented.

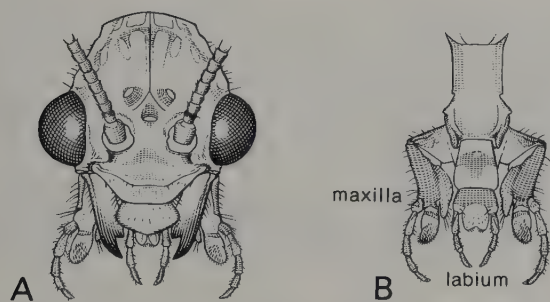
Thorax (Fig. 32.1). All segments well developed and freely movable. Pronotum large, subrectangular or trapezoidal. Meso- and metathorax similar in shape, with distinct postnota and normal spiracles.

Legs. Strongly developed, similar; coxae rather short, mid and hind coxae basally enlarged; each tarsus 5-segmented, ending in 2 generally simple claws, and without pulvillus, although 4th tarsal segment of Sialidae laterally and ventrally expanded and functioning as a pulvillus.

Wings (Fig. 32.5). Membranous, slightly dissimilar; hind wing with an expanded, foldable anal field. Venation complete, with no or very little end-twigging of longitudinal veins. Sc and R₁ fused towards wing apex; R₂₊₃ may be pectinately branched; M of fore wing generally 2-branched in Australian Corydalidae, 3-4-branched in Australian Sialidae; CuA generally branched in both fore and hind wing. Jugal lobe distinct with well-developed jugal vein in Corydalidae; lobe not developed, and with

Fig. 32.1 *Archichauliodes* sp., Corydalidae.

[T. Binder]

Fig. 32.2 *Archichauliodes* sp.: A, head, frontal; B, maxillae and labium, ventral.

[M. Quick]

only a faint jugal vein in Sialidae. Wing coupling by jugal region of fore wing overlying humeral region of hind wing; no special frenular hairs.

Abdomen. Very soft and flexible, segment 1 with some sclerotisation. Spiracles on segments 1–8. Females of some Corydalidae have a sternal pouch which is a semi-circular membranous structure of unknown function opening in the intersegmental membrane behind S6. In male (Figs 32.3A, B) T9 generally hooded and slightly more heavily sclerotised than preceding tergites; gonocoxites and gonostyli (lateral plates) articulating at ventral margins of T9 in Sialidae and Corydalinae but absent in Chauliiodinae; S9 modified into subgenital plate; T10 forming terminal plate or pair of anal claspers, these simple or bifurcate and often with sensilla (trichobothria); S10 represented by, at least, fused gonocoxites and styli, and generally termed aedeagus in Corydalidae, gonarcus

or genital plate in Sialidae. In female (Figs 32.3C, D) S8 more or less strongly modified as a subgenital plate; T9 produced ventrolaterally with a pair of gonocoxites ('gonapophyses') attached posteroventrally to form the ovipositor, gonostyli either articulated with posterior tip of gonocoxites or fused with them (Fig. 32.3D). T10 medially divided by anus, forming pair of cercoid anal plates often with a group of sensilla. Egg-pore and copulatory pore independent.

Internal anatomy. Central nervous system consisting of 3 thoracic and generally 7 abdominal ganglia. Digestive system with median, dorsal food-reservoir, peritrophic membrane, and 6 or 8 Malpighian tubules. In male *Sialis* a pair of testes composed of 6 follicles communicates with a common ejaculatory duct by paired vasa deferentia provided with seminal vesicles; accessory glands present (Handlirsch and Beier 1936). Female with ovaries consisting of variable number of panoistic (Corydalidae) or telotrophic (Sialidae) ovarioles; bursa copulatrix and spermathecal duct of variable shape; accessory glands present or absent (Glorioso 1981).

Immature Stages

Egg. Dark brown and cylindrical with the ends roughly rounded. Length 0.2–1.7 mm. Eggs are attached by one end or one side, and the free end has a generally conspicuous micropylar apparatus of variable form (white, elongate, terminally clubbed in *Archichauliodes*).

Larva (Fig. 32.6). Elongate and flattened. Head (Figs 32.4A, B) prognathous; labrum and clypeus distinct; mouth-parts biting; mandibles stout, powerful and sharply

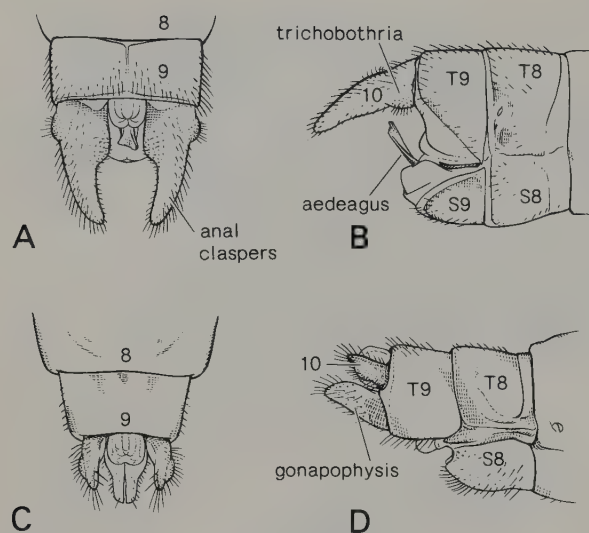


Fig. 32.3 Terminalia of *Archichauliodes* spp.: A, ♂, dorsal; B, ♂, lateral; C, ♀, dorsal; D, ♀, lateral. [M. Quick]

toothed; maxillae elongate with 5-segmented palps; labium consisting of mentum, denticulate ligula and 3-segmented palps; gular plate distinct and large. Eyes with separate stemmata (6 in *Archichauliodes*). Antennae prominent, 4–5-segmented. Prothorax large, pronotum and prosternum both heavily sclerotised; mesonotum and metanotum wider than long, sclerotised; spiracles present on all thoracic segments; legs with unsegmented tarsi terminating in paired claws. In Sialidae, abdominal segments 1–7 each with pair of 4–5-segmented, lateral filaments (tracheal gills); each filament with many long setae; segment 10 with long, tapering, median filament. In Corydalidae, segments 1–8 each with pair of 2-segmented tapering, lateral filaments with a few short setae; segments 1–7 often with tuft of accessory tracheal gills at base of each gill; segment 10 with pair of large prolegs, each with a lateral filament and 2 large, terminal claws. Spiracles present on segments 1–8, although very small in Sialidae; spiracles of segment 8 pedunculate in some Corydalidae. Spiracles closed while larvae are in water.

Pupa. Active, denticous, exarate, similar to that of some Coleoptera. Head similar to that of the larva, but with much greater development of antennae and compound eyes.

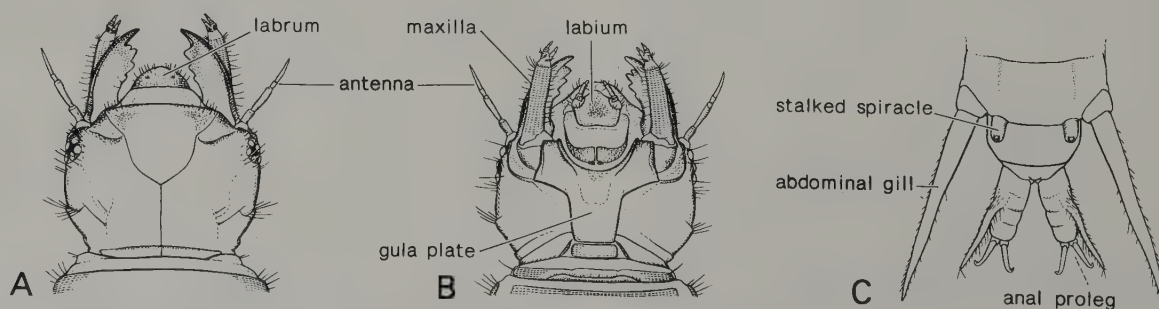


Fig. 32.4 Larva of *Archichauliodes* sp.: A, head, dorsal; B, head, ventral; C, apex of abdomen, dorsal. [M. Quick]

Biology

Adults. Megaloptera are common stream insects. The Australian species generally are associated with clear, cold waters, but at least some Corydalidae are known from swamps and some Sialidae from silty or muddy sections of slowly flowing streams. Adults emerge from late spring to autumn, are short lived and take very little food. During the day they are usually found resting on stems of plants bordering larval habitats. Corydalidae rest with the wings folded flat over the abdomen, the anal area of the hind wing being folded under the remainder of the wing; Sialidae rest with the wings steeply roof-like, as in most Neuroptera and Trichoptera. A few species of Megaloptera are very active in bright sunlight; others fly only in dull daylight. Probably all Australian species are to some extent crepuscular or nocturnal and all are attracted to lights. The flight of Corydalidae is generally awkward, slow and irregular but may be swift when the insect is disturbed. Both sexes of Australian *Archichauliodes* glide high over streams with wings outspread, slightly swept back and raised above the horizontal, and dip to the water surface occasionally, but the significance of these activities is unknown. Corydalidae often exude a whitish or pinkish fluid when handled.

Reproduction. Copulation takes place in vegetation near water. Premating communication between sexes by vibration signals has been described for Sialidae (Rupprecht 1975). Eggs are laid in compact masses of 200 to more than 3000 on vegetation or on rocks overhanging or projecting from water, generally in positions protected from the sun during the hottest part of the day. Many females aggregate for oviposition; their conjoined egg-masses cover considerable areas and resemble lichens encrusting the rock. Freshly laid eggs are pale; they quickly darken and hatch in 1–4 weeks.

Immature Stages. After hatching larvae drop into the water and sink to the bottom. They live under rocks and debris and are active predators, feeding on a wide variety of small, aquatic invertebrates. The life cycle occupies 1–5 years with larvae passing through 10–12 instars. Fully grown larvae of *Archichauliodes* disperse to high water marks in spring and early summer and after the water recedes are left on the banks. There they construct a simple chamber in the soil or litter and may remain in the active larval stage for several months before pupation takes place. The pupal stage lasts only a few weeks (Hamilton 1940).

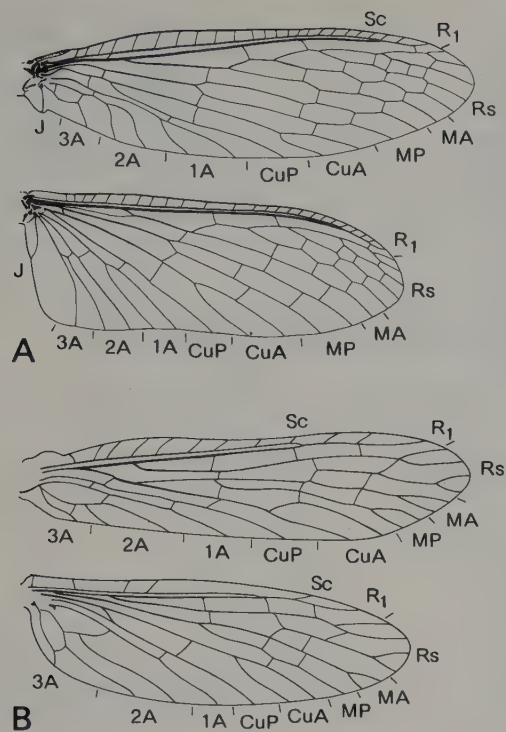


Fig. 32.5 Wing venation: A, *Archichauliodes* sp., Corydalidae; B, *Stenosialis* sp., Sialidae. [M. Quick]

Natural Enemies. Adult and larval Megaloptera are preyed upon by birds, bats, frogs, tortoises and fish; females are particularly endangered when ovipositing. Eggs are sometimes parasitised by Trichogrammatidae (HYMN); corydalid eggs are eaten by adults and larvae of Anthicidae (COLE).

Economic Significance. Larvae are both predators and prey of other stream animals and are a significant link in

food chains. *Archichauliodes diversus* from New Zealand is said to be economically important as trout food; its larva is much esteemed as bait (Tillyard 1921b). In Japan dried larvae of some Corydalidae ('magotaro-mushi') are believed to be a remedy for infant emotional irritation (Kuwayama 1962).

Special Features of the Australian Fauna

The 26 known Australian species, all of which are endemic, constitute about 10% of the known world fauna. In Australia species are restricted to the higher rainfall regions of the east and extreme south-west.

Both genera of Australian Sialidae, *Austrosialis* and *Stenosialis*, are apparently endemic although similar to some South American, South African and Indian genera. Australian Corydalidae are assigned to one of two genera: *Archichauliodes*, also represented in New Zealand and Chile and *Protochauliodes*, known also from Chile and western North America. These distributions show the overwhelmingly southern affinities of the Australian fauna. Adults of the *anagaurus* species group of *Archichauliodes* are more similar to adults of New Zealand and South American *Archichauliodes*, than they are to adults of any of the other four, endemic Australian species groups of *Archichauliodes* s.str. or to adults of the monotypic subgenus *Apochauliodes* which is endemic to W.A. There are significant morphological differences between the adults of North American, Chilean and Australian *Protochauliodes* and it is likely that a future comprehensive treatment of the world fauna of Megaloptera will result in a higher taxonomic ranking of some species groups.

Of particular interest is the existence of no fewer than 14 species of Megaloptera (11 Corydalidae, 3 Sialidae) in the comparatively small area of tropical, north-eastern Qld. There are no records of Megaloptera from New Guinea.

CLASSIFICATION

Order MEGALOPTERA
(26 Australian spp.)

- 1. Sialidae (4)
- 2. Corydalidae (22)

The two widely recognised families, the Sialidae and the Corydalidae, generally are considered sister groups. The clearly separable subfamilies of the Corydalidae,

the Corydalinae and the Chauliodinae, have been given family rank by some authors.

Key to the Families of Megaloptera

ADULTS

- With 3 ocelli; 4th tarsal segment simple; fore wing 17–50 mm **Corydalidae**
- Ocelli absent; 4th tarsal segment prominently bilobed; fore wing less than 14 mm **Sialidae**

LARVAE

- Abdomen with 8 pairs of lateral gills; apical segment of abdomen with pair of prolegs but without terminal filament (Fig. 32.6B) **Corydalidae**
- Abdomen with 7 pairs of lateral gills; apical segment of abdomen without prolegs but with terminal filament (Fig. 32.6A) **Sialidae**

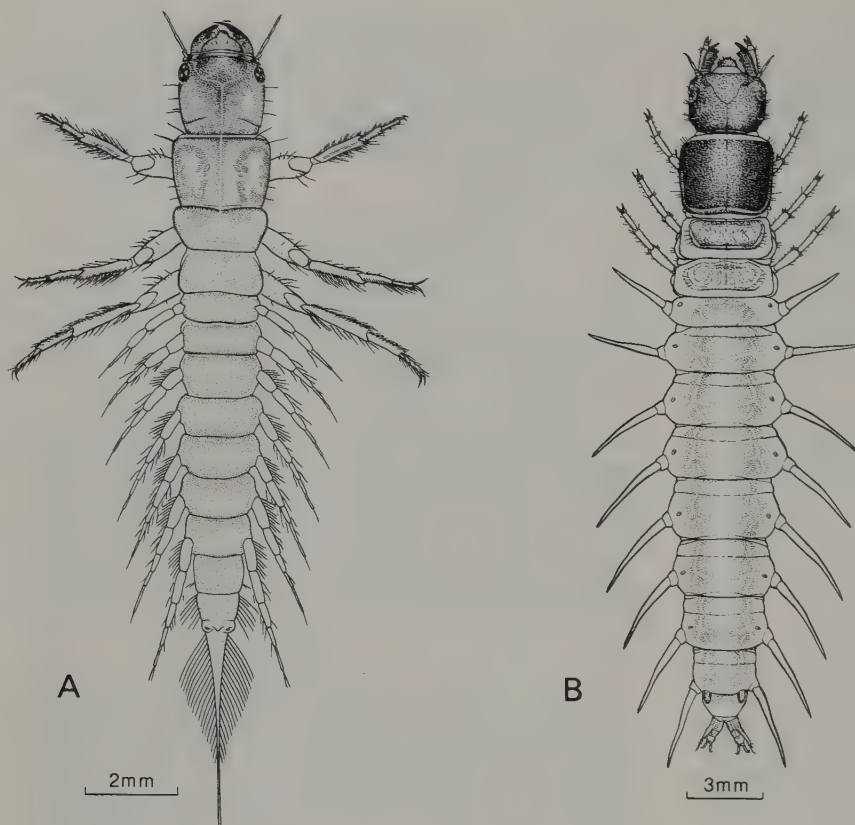


Fig. 32.6 Larvae: A, *Stenosialis* sp., Sialidae; B, *Archichauliodes* sp., Corydalidae.
[A by S. Smith; B by M. Quick]

1. Sialidae. The Australian species are small (fore wing 9–14 mm) and dark brown to grey. *Austrosialis* and *Stenosialis* differ in wing venation and female genitalia. One species of *Austrosialis* is known only from Tas., the other from north-eastern Qld. One species of *Stenosialis* ranges throughout the more coastal ranges of eastern Australia from Cape York to southern Vic., whereas the second species has been found in only a few localities in north-eastern Qld (Theischinger 1983).

2. Corydalidae. All Australian species are placed in the subfamily CHAULIODINAE in which the head of adults is subtriangular and without a posterolateral spine, and in which there are only 3 cross-veins between R and Rs.

Australian *Archichauliodes* are divided into 2 subgenera, *Apochauliodes* (1 sp.) with an unforked CuA in the fore wing, and *Archichauliodes s.str.* (19 spp.). *Archichauliodes (Apochauliodes) cervulus* is small (fore wing 18–29 mm) and is the only megalopteran known from W.A. Species of *Archichauliodes s.str.* are mostly larger (17–50 mm) and the subgenus is remarkably polytypic. Five distinct species groups can be recognised on genitalic structure and wing patterns (Theischinger 1983). The *anagaurus* group (2 alpine spp.) is closest to *Archichauliodes diversus* from New Zealand. The 4 species of the *guttiferus* group have a largely disjunct distribution

in eastern Australia (Watson and Theischinger 1984a). Three of the 4 species of the *polypastus* group are found in southern Qld and the remaining species ranges from north-eastern N.S.W. to eastern Vic. The *deceptor* group comprises a north-eastern Qld species, a more widespread species distributed from north-eastern Qld to south-eastern N.S.W., and an undescribed species from the Eungella area, Qld. The *uncinatus* group (5 spp.) is confined to tropical, north-eastern Qld, with one species recorded from the tip of Cape York Peninsula. The 3 Australian species of *Protochauliodes* are very similar in appearance and largely allopatric. *Protochauliodes kirramae* is sexually dichromic (males very dark, females almost white), and occurs in north-eastern Qld between about 16°S and 20°S. *Protochauliodes biconicus*, from eastern Qld south of about 26°S and eastern N.S.W., has geographically variable male genitalia. There is an undescribed *Protochauliodes* in the Eungella area.

ACKNOWLEDGMENTS. The use of information from Riek (1970, 1974a) is gratefully acknowledged. I am indebted to Dr U. Aspöck (Vienna, Austria) and to Dr O. S. Flint (Washington, D.C., U.S.A.) for valuable comments and criticisms of a draft of this chapter.

Raphidioptera

(Snake-flies, camelneck-flies)

H. ASPÖCK and U. ASPÖCK

Mandibulate, endopterygote Neoptera; antennae multisegmented; compound eyes always present; ocelli present only in Raphidiidae; prothorax elongate; with two pairs of subequal wings; ovipositor long. Larvae terrestrial; with biting mouth-parts and lateral ocelli. Pupae decticious.

The Raphidioptera is a small order of winged, terrestrial insects not found in Australia. Adults are of rather uniform appearance (Fig. 33.1), with fore wings ranging in length from about 5 to 20 mm. The order is supposed to be the sister-group of the Megaloptera and comprises two families, the Raphidiidae with 155 described species, and the Inocelliidae with 20. The total number of Recent species almost certainly does not exceed 200.

Raphidioptera are distributed throughout the Holarctic region, except for northern and eastern parts of North America, and the southernmost records are from Mexico, north-west Africa, Israel, northern India, Indochina and Taiwan. They are restricted to woodland habitats and occur in almost all Holarctic types of forests and forest-like habitats (e.g. orchards). In southern parts of their distribution they live mainly at higher altitudes (up to about 3000 m). The Southern Hemisphere lacks Raphidioptera entirely although unsuccessful attempts were made to introduce North American snake-flies into New Zealand and Australia in 1891. Reviews and comprehensive bibliographies can be found in Aspöck and Aspöck (1971), Aspöck *et al.* (1980), Aspöck (1986) and Aspöck *et al.* (in press).

Anatomy of Adult

Head (Fig. 33.3). Prognathous, flat, elongate, basally tapering or broad, extremely flexible, strongly sclerotised, sutures extremely reduced. Antennae filiform or (rarely)

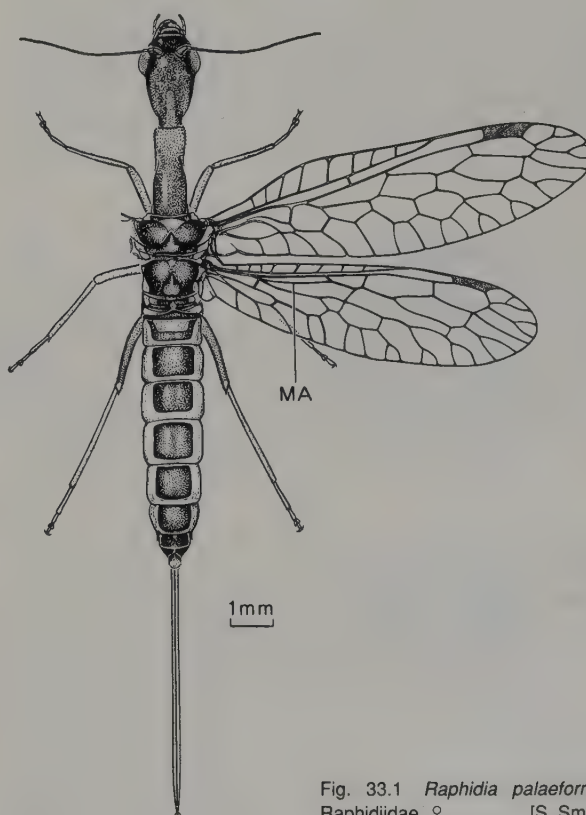
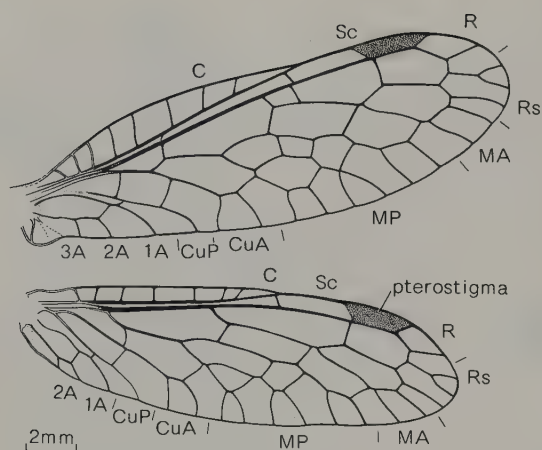


Fig. 33.1 *Raphidia palaeformis*, Raphidiidae, ♀. [S. Smith]

Fig. 33.2 *Parainocellia ressliei*, Inocelliidae, wings.

[S. Smith]

moniliform, multisegmented. Compound eyes large, situated laterally; with 3 dorsal ocelli (Raphidiidae), or without ocelli (Inocelliidae). Mouth-parts biting; mandibles with 3–4 teeth, each maxilla with cardo, stipes, lacinia, galea and 5-segmented palp; labium with submentum, prementum and 3-segmented palp; glossae and paraglossae lobed; hypopharynx with sclerotised clasps.

Thorax. Prothorax remarkably elongate particularly in Raphidiidae, very mobile (hence the common name, 'camelneck-flies'); coxae articulating at its posterior end; pronotum shield-like (Inocelliidae) or tube-like, laterally covering the pleural region (Raphidiidae); basisternum and furcasternum well developed. Meso- and metathorax similar, each with a pair of spiracles; nota divided into scutum, scutellum and postnotum; mesonotum with acrotergite; pleura with pleural suture, subalare separated from epimeron, pleural cleft dividing anepisternum from katepisternum and trochantin; coxae closely approxi-

mated, furcasternum (sternellum) and basisternum small, with deeply invaginated median suture.

Legs. All pairs similar, cursorial; mid and hind coxae with meron; tarsi 5-segmented, 3rd segment heart-shaped, dilated, 4th reduced, 5th with 2 very small claws.

Wings (Figs 33.1, 2). Membranous, hyaline, subequal, elongate, pterostigma coloured; wing-coupling by bristles of the jugal and humeral lobe; at rest wings in roof-like position; venation simple, with few cross-veins; basal portion of MA in the hind wing either a longitudinal vein (both families), cross-vein (many Raphidiidae) or cryptic (most Inocelliidae).

Abdomen. Consisting of 10 (visible) segments, the anterior 2 partly reduced and sclerites fragmentary; more posterior segments with simple tergal and sternal plates; pleura membranous; segments 1–8 each with a pair of spiracles. Male genitalia (Figs 33.4A–D) extremely complex. In most genera 9th segment ring-like; gonocoxites shell-shaped (Inocelliidae) or very diverse, with articulating stylus and often with prominent apex (Raphidiidae); ventrally membranous (Inocelliidae) or sclerotised (hypovalva of Raphidiidae); ectoproct (T10 + T11) usually with trichobothria. The typical internal sclerites are: parameres (= arcessus of Inocelliidae), a gonarcus, and hypandrium internum; endophallus with sclerotised accessory differentiations. Female (Figs 33.1, 4E) with long, flexible ovipositor formed by the dorsally-connected, paired 3rd (+ 2nd) valvulae of the 9th segment (with terminal styli) and the unpaired 1st valvulae of the 8th segment which together enclose the tubular egg duct.

Internal Anatomy. Studied in very few species only. Alimentary canal with salivary pump; paired salivary glands reaching into metathorax; oesophagus long; crop with large dorsal diverticulum; 6 Malpighian tubules, 4 of them extending to colon; rectal papillae well developed. Central nervous system with 3 thoracic and 8 abdominal ganglia (1st abdominal ganglion not fused with metatho-

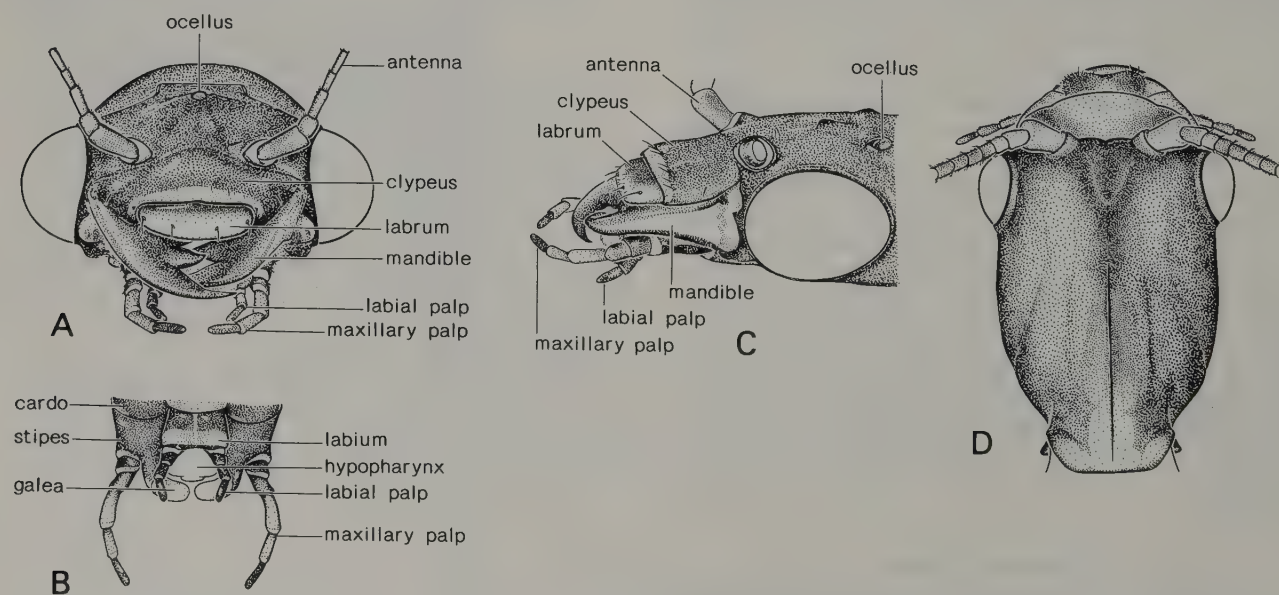


Fig. 33.3 Heads, mouth-parts of *Raphidia palaeformis*, Raphidiidae, and *Parainocellia ressliei*, Inocelliidae: A, *R. palaeformis*, head, anterior; B, *R. palaeformis*, mouth-parts, ventral; C, *R. palaeformis*, head, lateral; D, *P. ressliei*, head, dorsal.

[S. Smith]

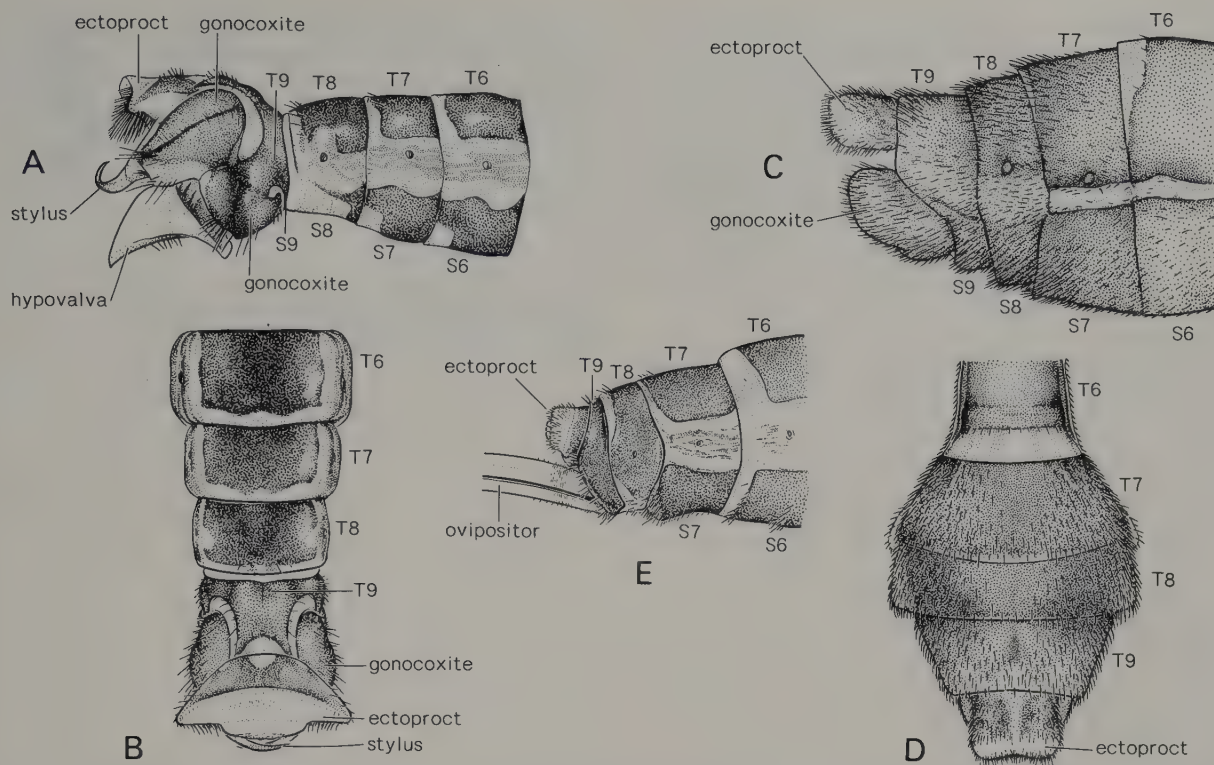


Fig. 33.4 Terminalia of *Raphidia palaeformis*, Raphidiidae, and *Parainocellia ressl*, Inocelliidae: A, B, *R. palaeformis*, ♂, lateral and dorsal; C, D, *P. ressl*, ♂, lateral and dorsal; E, *R. palaeformis*, ♀, lateral. [S. Smith]

racic one). Male: paired testes with about 12 follicles, in the 6th and 7th segments; paired, narrow vasa deferentia with seminal vesicles and large paired glands; unpaired

ejaculatory duct opening caudally with gonopore on endophallus. Female: ovaries paired, grape-like, with about 40 telotrophic ovarioles; lateral oviducts uniting to common oviduct, which accepts seminal duct and thereafter becomes the vagina. Bursa copulatrix consisting of the usually membranously-pouched, sometimes partly sclerotised atrium bursae and sacculus bursae; seminal receptacle with paired glands and narrow seminal duct.

Immature Stages

Egg. Elongate-oval, yellowish white with prominent micropyle knob; 1.4–1.7 mm long, 0.25–0.50 mm broad.

Larva (Fig. 33.5). Elongate, flattened; head prognathous with 4–7 stemmata; mouth-parts biting; head and the only moderately elongate prothorax strongly sclerotised; 10 abdominal segments; mid gut open during larval period; number of larval instars variable, usually 10–15.

Pupa. Always decticious.

Biology

Adults are active by day; they prey on soft-bodied arthropods and also feed on pollen. There is a long courtship before mating and during copulation the male is beneath the female. Females oviposit under bark or in similar situations. Each female lays up to 800 eggs in clusters of a few to well over 100 cemented together. Larvae are terrestrial and live under bark or in litter where they also prey on soft-bodied arthropods. The life-cycle usually occupies two years, rarely one year, sometimes three or more. The last hibernation is mostly as a larva or (as in

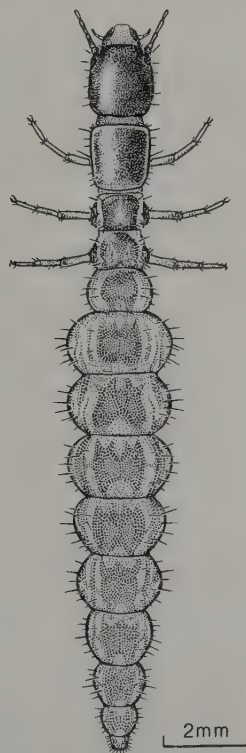


Fig. 33.5 Larva of *Phaeostigma robusta*, Raphidiidae.

[S. Smith]

some Raphidiidae) as a pupa. Low temperatures are essential for the initiation of the prepupal phase or for moulting to the adult stage. The pharate adult (the active pupa) is very mobile.

Many species regularly develop high population densities. At such densities adults and larvae are effective predators on phytophagous arthropods and are of eco-

nomic importance in forests, orchards etc. The most frequent parasitoids of raphidiopteran larvae, at least in the Western Palaearctic, are species of *Nemeritis* (HYMN: Ichneumonidae); other genera of Ichneumonidae and of Braconidae (HYMN) are less common natural enemies. Hyperparasitism by species of Perilampidae (HYMN) is relatively frequent.

Neuroptera

(Lacewings)

T. R. NEW

Endopterygote, mandibulate Neoptera; antennae multisegmented, filiform, moniliform or variously thickened, usually conspicuous; compound eyes always present; ocelli usually absent; generally two pairs of large, equal or subequal membranous wings, often with numerous cross-veins; main veins usually with 'end-twiggings'; trichosors often present. Larvae with distinctive sucking jaws, usually campodeiform and free living. Pupation in silken cocoon; pupae decticus.

The Neuroptera, or Planipennia, is one of the most archaic groups of endopterygote Neoptera. Adults (Figs 34.1, 2) range from very small insects with a wing-span of about 5 mm to very large forms with wing-span exceeding 150 mm. Although many are cryptically coloured, others are brightly coloured and patterned, and many are clothed with long, dense hairs. Some taxa are very swift fliers (Ascalaphidae, in particular) but most fly rather slowly and irregularly and in these the wing-coupling mechanism, if present, appears inefficient. Sexual dimorphism is generally slight, but is especially marked in some Ascalaphidae in which males have a dorsal abdominal process (Fig. 34.2D). There are differences in wing shape between the sexes of some Hemerobiidae and Chrysopidae and the berothid *Trichoma*. Most lacewings are recognisable by their having the main veins branched (or 'twigged') at the end, and by the way they hold their wings in a steep 'roof' while at rest.

The Neuroptera is a small order, with a little more than 5000 described species. It is represented in all major zoogeographical regions, usually being more abundant in the tropics than in temperate areas. Neuroptera occur throughout Australia. Globally, some of the families are geographically limited, and many are small, some having only a few tens of species. The largest families are Chrysopidae and Myrmeleontidae, each with around 2000

described species. The immature stages of Neuroptera were discussed by Withycombe (1925) and a synopsis of larval forms is given by Gepp (1984). Recent revisions have considerably improved knowledge of the Australian fauna (e.g. Aspöck and Aspöck 1984, 1985, 1986; Lambkin 1986a, b; Mansell 1983; New 1980–89a; Riek 1974b, 1976e), and the biology of the order is reviewed by New (1986d). A more extensive, general account of the order is given by New (1989b).

Anatomy of Adult

Head (Fig. 34.3A). Usually transverse, orthognathous or more or less hypognathous. Clypeus and labrum elongate in Nemopteridae. Hind margin deeply excavated in Ascalaphidae. Compound eyes large, usually bare. Ocelli absent except in Osmylidae, where they are sometimes poorly defined. Antennae multisegmented, usually filiform and tapering, pectinate in the male of the non-Australian Dilaridae and sometimes longer than wings; scape large, succeeding 1 or 2 segments sometimes enlarged. There is some tendency for both shortening and broadening to occur, so that the apex is thickened, or incipiently clubbed in Ascalaphidae and Myrmeleontidae. More uniform thickening occurs in many Mantispidae, and enlargement and/or ornamentation of the moniliform flagellar segments occurs in males of some

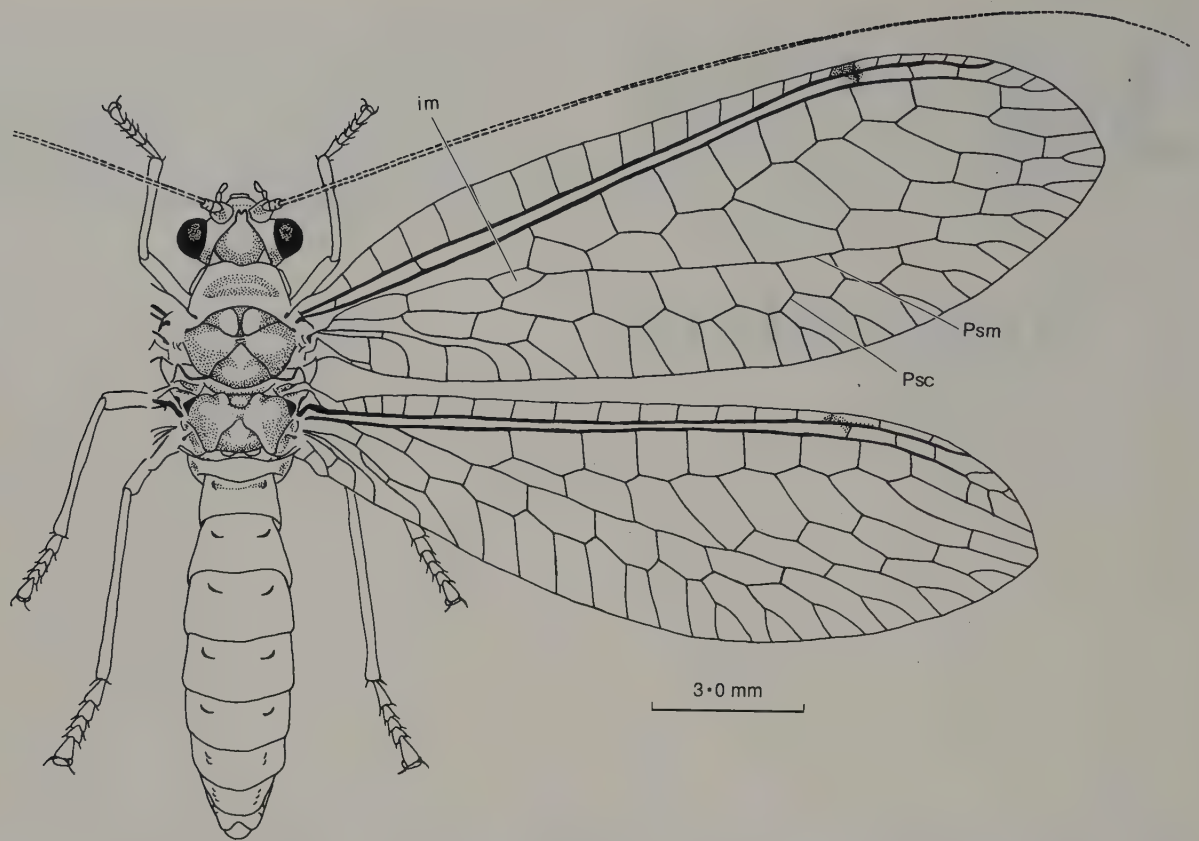


Fig. 34.1 *Chrysopa s. l. sp.*, Chrysopidae, ♂ (im, intramedian cell; Psc, pseudocubitus; Psm, pseudomedia).

[T. Binder, T. Carpenter]

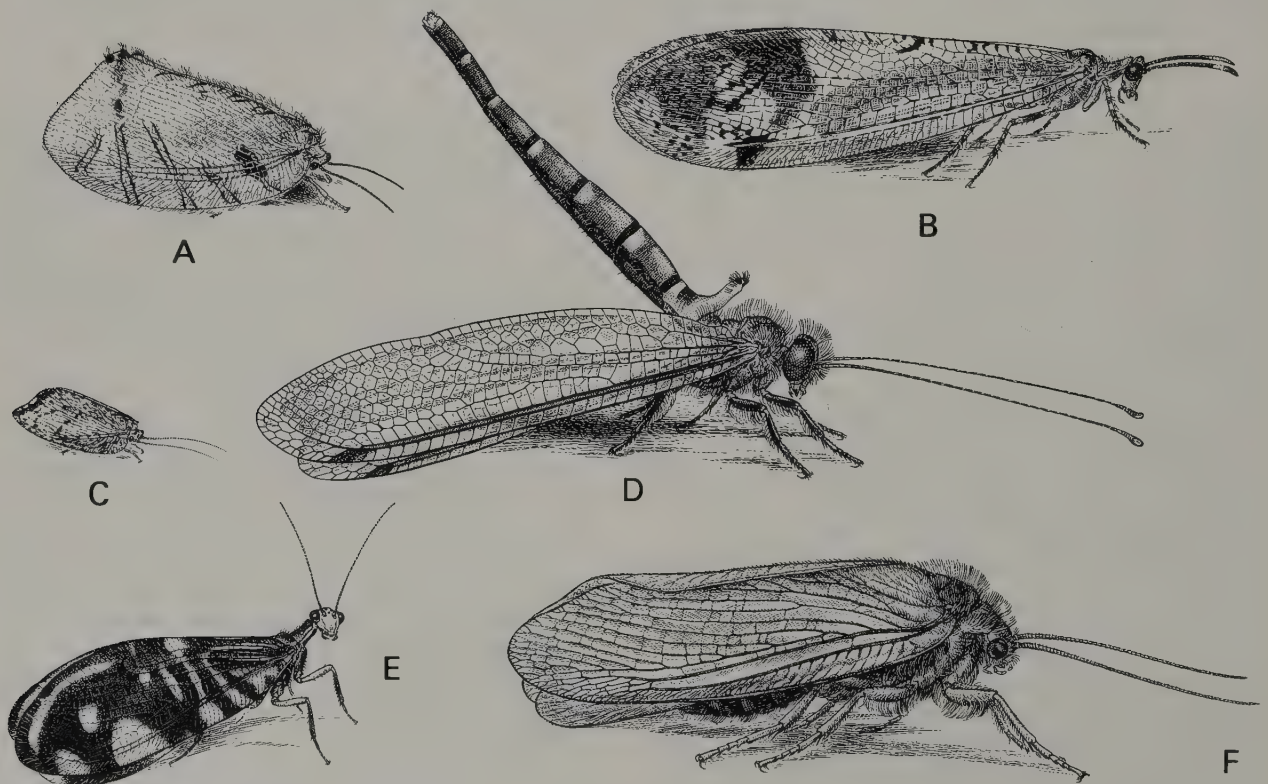


Fig. 34.2 Adults in resting position: A, *Psychopsis mimica*, Psychopsidae; B, *Glenoleon pulchellus*, Myrmeleontidae; C, *Drepanacra binocula*, Hemerobiidae; D, *Megacmonotus magnus*, Ascalaphidae; E, *Porismus strigatus*, Osmylidae; F, *Megalithone megacerca*, Ithonidae.

[M. Quick]

Coniopterygidae. Mouth-parts simple, biting; maxillary palps (Fig. 34.3C) normally 5-segmented; labial palps (Fig. 34.3B) 2- or (more commonly) 3-segmented; ligula reduced to median process, sometimes slightly bilobed, or absent. The apical segment of at least 1 pair of palps is usually enlarged and in some Myrmeleontidae there is a well-defined groove presumed to contain sensilla.

Thorax. Prothorax freely movable; generally transverse or slightly longer than broad, but relatively longer in many Osmylidae and very long and narrow in Mantispidae (Fig. 34.3D). Mesothorax and metathorax usually well developed, and of similar size (metathorax reduced in Nemopteridae).

Legs. Mostly unelaborated and cursorial, but fore legs strongly raptorial in Mantispidae (Fig. 34.3D) and some non-Australian Berothidae (Rhachiberothinae). Fore coxae often elongate, and with raised setae in some Osmylidae. Hind trochanter apically produced on inner edge except in Myrmeleontoidea. Tibiae with or without apical spur or spurs; femora and/or tibiae rarely expanded and slightly flattened. Tarsi 5-segmented, ending in 2 claws except the fore leg of some Mantispidae. The claws may be very long, may have 1 or more subapical teeth and (rarely) are opposable on the tarsus. Some Mantispidae have claws with up to 6 terminal spines. Empodium simple or bilobed.

Wings (Figs 34.7, 8). Generally 2 pairs of equal or subequal wings, with full and complex venation. Hind wings of Nemopteridae (Fig. 34.8G) are very long and narrow, and differ markedly from the short fore wings. In Ithonidae (Fig. 34.7A), the hind wing is more expanded in the anal region than the fore wing. The hind wing is reduced in some Hemerobiidae and Coniopterygidae. Sexual dimorphism is uncommon; males of some Chrysopidae and Hemerobiidae have thickened veins and in *Chrysopa* (*Mallada*) *basalis* these form a thickened pterostigma which is struck on the substrate during courtship. Some Osmylidae have a thickened posterior spot on the fore wing and 'embossed' areas of wing membrane occur in some Psychopsidae. In a few families, the number of vein branches and cross-veins is low (Coniopterygidae, Fig. 34.7E; Sisyridae, Fig. 34.7G). Many fore wing costal cross-veins occur in all families except Coniopterygidae (which have no more than 2) and the pterostigma is usually at least indicated and often very well defined (Ascalaphidae, Mantispidae). Fusion between parts of some of the main longitudinal veins is responsible for the very distinctive zig-zagged venation of Chrysopidae (Figs 34.1, 8B, C).

Small circular spots (*nygmata*) are sometimes present and are presumed to be sensory. They occur between the posterior 2 branches of the apparent Rs, rarely behind the posterior branch, and/or basally between Rs and M. The wing margin often has a fringe of hairs or a series of marginal thickenings (*trichosors*) each bearing hairs. There may be 1 trichosor between each pair of veins and branches around the wing perimeter. The wing veins themselves may be haired and some Berothidae have thickened scale-like hairs on some veins. The wing membrane is more or less scattered with minute microtrichia,

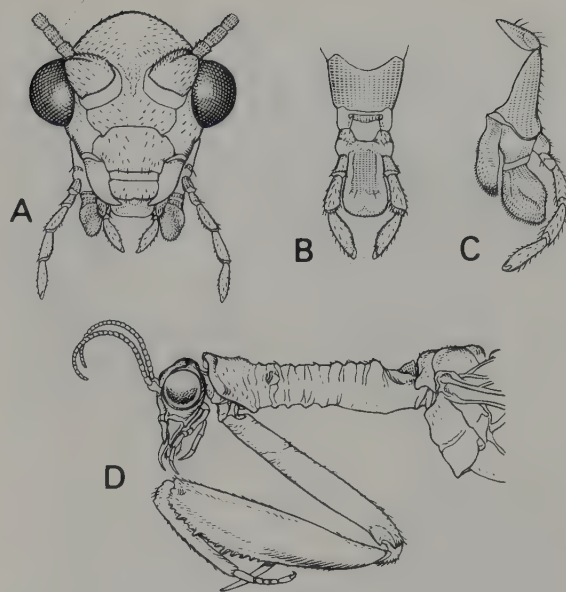


Fig. 34.3 Head of *Dictyochrysa* sp., Chrysopidae: A, frontal; B, labium, ventral; C, maxilla, ventral. D, head and prothorax of *Campion* sp., Mantispidae, lateral. [M. Quick]

but in many families it appears glabrous at normal magnifications. Males of many Myrmeleontidae have a posterior clavate projection (*axilula pilaris*) at the hind wing base. This is a scent-dispersive surface associated with thoracic glands. In males of some Nemopteridae there is a bulla at the base of the fore wing and (sometimes) another type of bulla at the base of the hind wing; both have modified, silky, probably sensory hairs.

Wing coupling is usually simple, and may involve a simple frenulum-coupling (as in Hemerobiidae) in which an expanded jugal lobe at the base of the fore wing couples with a small, basal, costal, hind wing process bearing a few enlarged bristles. The jugal lobe is reduced in many families and in some of these, thickening of postero-marginal veins of the fore wing may aid coupling. Coniopterygidae are unusual in that the anterior margin of the hind wing bears hamuli-like bristles, and the fore wing jugal region has a series of hooks. The former link with the anal region of the fore wing and the latter with the basal length of R in the hind wing, providing firm wing-coupling.

Abdomen. Ten-segmented, with only 9 distinguishable segments in Chrysopidae, and S1 generally strongly reduced. Usually cylindrical, but broadened around segments 3–5 in males of Stilbopteryginae (and with the tergites sometimes ornamented), and males of many Ascalaphidae have a dorsal process on segment 2 or 3.

The terminalia are modified and specialised in both sexes, and the various parts of the genitalia are difficult to homologue between the families. They are discussed by Acker (1960), Adams (1969), Tjeder (1970) and Aspöck *et al.* (1980) and recent taxonomic papers indicate the range of structures present. Apparently only Coniopterygidae retain a true penis. A long ovipositor occurs only in Dilaridae and some Mantispidae (not in

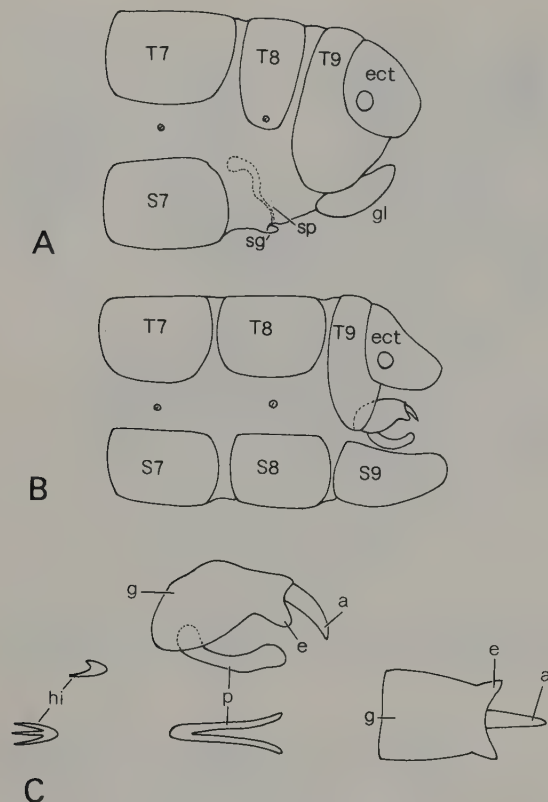


Fig. 34.4 Terminalia of generalised hemerobiid, to indicate terminology used in descriptions: A, ♀, lateral; B, ♂, lateral; C, ♂, genital complex lateral (upper) and ventral (lower).

[A. Hastings] a, arcessus; e, entoprocessus; ect, ectoproct; g, gonarcus; gl, lateral gonapophysis; hi, hypandrium internum; p, paramere; s, sternite; sg, subgenital; sp, spermatheca; T, tergite.

Australian species). Generalised descriptive terminology is indicated in Fig. 34.4.

Internal anatomy. Not well known, although outlined in general terms in several early accounts. Gut usually simple, although a dorsal fore gut diverticulum present in some groups. Usually 8 Malpighian tubules; 6 in Coniopterygidae. Three thoracic and 7 abdominal ganglia.

A spermatophore is said to be usually involved in mating, but it is absent in Coniopterygidae and many Chrysopidae, and its presence has not been confirmed in several other families. The female has polytrophic ovarioles, and in some New World Ascalaphidae the anterior ones are specialised for production of *repagula* (aborted eggs which help to protect the viable eggs from predators such as ants).

Immature Stages

Egg. Usually elongate oval, more rarely almost spherical. The micropyle is well defined, and usually represented by a raised knob or plate. There appears to be a micropylar plate at both ends of eggs of Myrmeleontidae and Ascalaphidae, but this is exceptional in the order. The chorion usually has at least traces of areolate, pentagonal or hexagonal sculpturing and in some osmylids and nemopterids has pronounced papillae.

Hatching usually occurs through use of a larval ovipositor to make a longitudinal slit, but in many Myrmeleontoidea this structure is absent and there is a circular 'line of weakness' which enables the 'top' of the egg to be pushed off.

Larva. The general form (Figs 34.9–12) is an active, predatory, campodeiform larva, with conspicuous, protruding jaws. Rarely, associated with more sedentary feeding habits, a more scarabaeiform larva occurs, as in the subterranean Ithonidae and parasitic Mantispidae. Some ground-dwelling larvae possess long, curved hairs or setae, sometimes grouped on raised tubercles, and those of *Nymphes* and many Chrysopidae have tangling filaments, all of which entrap debris on the dorsal surface, aiding concealment. There are well-defined lateral processes on the thorax and abdomen of many Myrmeleontoidea, and their arrangement has considerable taxonomic value. Ascalaphidae, in particular, have heavily ornamented papillae (*dolichasters*) on the body.

Tarsi are 1-segmented, and there are normally 2 tarsal claws. In some groups of Myrmeleontoidea, the hind tibia and tarsus are fused into a single structure, presumably more efficient for backwards movement. The mandible and maxilla of each side fit together to form a sucking tube. The maxilla is a stylet and the maxillary palp is absent. Labial palps are usually well defined, but absent in Sisyridae. The labrum is reduced, except in Coniopterygidae.

The abdomen may end in 'suction discs', which occasionally contain hooked spicules.

The mid gut is separated from the hind gut, so that no faecal material is passed by the larva until pupation.

Pupa. Decticus and exarate, with the head and abdominal apex curved ventrally in the cocoon. The cocoon is silken, but can incorporate other material such as sand grains or fragments of vegetation. The pupal mandibles are strongly sclerotised, usually sharply pointed and with one or more medial teeth. They may be asymmetrical, as in many Chrysopidae, and normally cross slightly in the midline.

Biology

Adults. The distribution of Neuroptera reflects the habits and habitats of the larvae. Australian species are found in most ecosystems, ranging from desert regions to cold, subalpine stream margins, although few species occur in either of these extremes. Sisyridae are most commonly collected close to fresh water, as are some Osmylidae (such as Kempyninae) with semiaquatic larvae. Other osmylids, with arboreal, subcortical larvae, occur in open forest habitats. Psychopsidae are also predominantly forest insects, mainly in the wetter, eastern coastal zone. Berothidae appear to be more abundant in drier regions; habitats of most larvae of this family are unknown. Chrysopidae, Hemerobiidae and Coniopterygidae are more generally distributed, wherever small soft-bodied prey such as aphids and psyllids are numerous. Ithonidae and many Myrmeleontidae occur most commonly in areas with sandy or friable soil, and

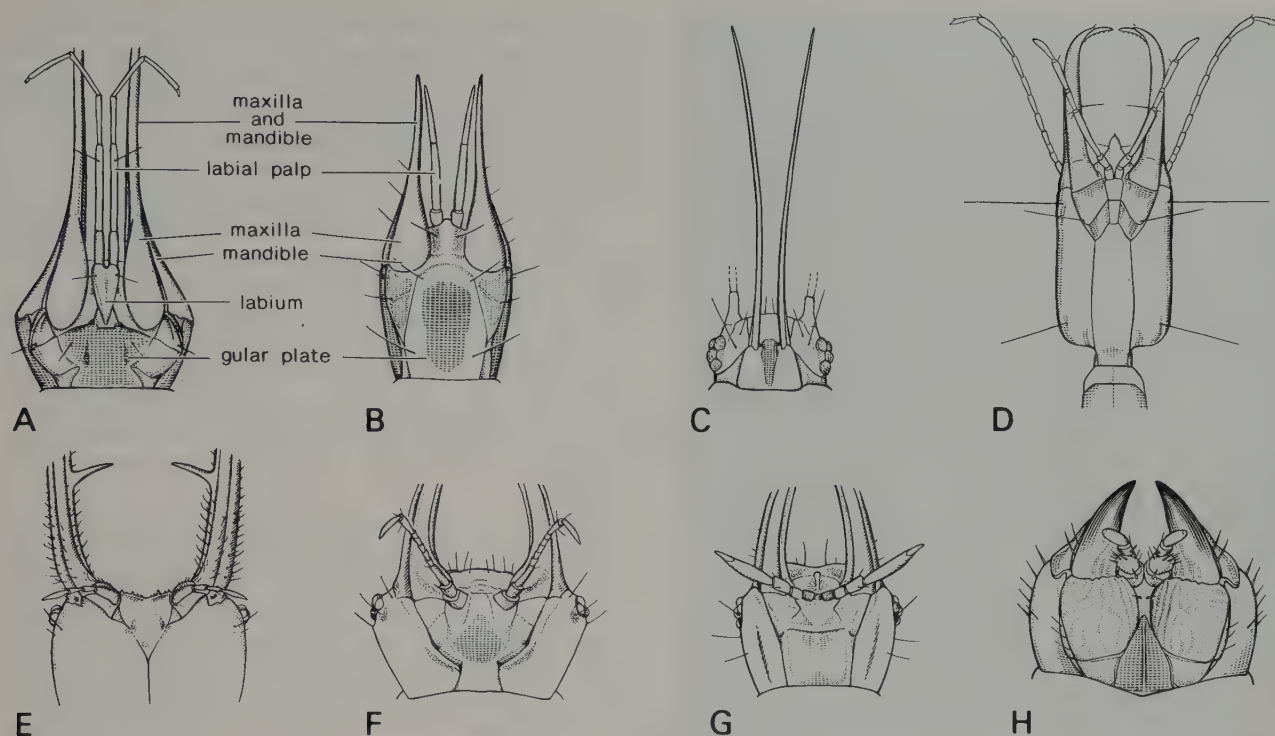


Fig. 34.5 Heads of larvae, ventral: A, *Porismus strigatus*, Osmylidae; B, berothid; C, *Sisyra* sp., Sisyridae; D, *Austroneurorthus* sp., Neurorthidae; E, myrmeleontid; F, *Chrysopa* sp., Chrysopidae; G, hemerobiid; H, *Ithone* sp., Ithonidae. [M. Quick]

Nemopteridae are limited to drier areas. The pit-forming species of Myrmeleontidae tend to seek out sheltered and dry habitats, areas where larval pits can be constructed most successfully.

Most adult lacewings have been presumed to be predators, and many undoubtedly are so. Some Chrysopidae, though, are specialised honeydew feeders, and examination of gut contents has shown that members of many other families may be, at least casually, omnivorous or phytophagous. Some Nemopteridae, Myrmeleontidae, Sisyridae and Osmylidae clearly take non-animal food at times.

Many larger Neuroptera emit distinctive scents when handled. Some chrysopids have been termed 'stink-flies', and their pungent odours are presumably defensive. Sexual scents are produced by members of several families, often through specialised, abdominal structures. Male *Nymphes myrmeleonides* produce a musk-like odour from an eversible gland opening between S6 and S7. Males of some Mantispidae have a scent gland between T5 and T6; males of Neurorthidae and some Myrmeleontidae have eversible, sac-like structures (*pleuritocava*) on the abdomen. The thoracic glands and hind wing axilula pilaris of some Myrmeleontidae were mentioned earlier. Hair-pencils occur in males of most Australian Myrmeleontidae: Acanthaclisinae. *Myiodactylus* (Nymphidae) gives off 'an ant-like smell that is also a little like rancid coconut' (Riek 1970); the function of this is not clear.

Sound production by one or both sexes also plays a role in the courtship of some lacewings. Henry (1984) showed that sibling species of North American

Chrysopidae may produce markedly different sound patterns, made by tapping the abdomen on the substrate.

Reproduction. Swarming aggregation has been recorded in Ithonidae, and is presumed to represent mass emergence or mating flights. Isolated exotic species of Coniopterygidae and Myrmeleontidae have also been recorded swarming, but this appears to be rather unusual. In most other lacewings, adults emerge over a longer period. Many species are attracted to light. Some brightly coloured lacewings are diurnal, but more species appear to be crepuscular or nocturnal. Aggregations of Osmylidae have been found near stream margins, and mantispid females may oviposit communally. The sex ratio is usually close to 1:1, although male ithonids greatly outnumber females in emergence flights.

Generation time ranges from a few weeks to a few years, with most species at least univoltine.

Immature Stages. Eggs may be laid singly, or in batches, and may be scattered in or on sand (Ithonidae, Myrmeleontidae) or cemented to a substrate. In most Chrysopidae, Nymphidae, Berothidae and Mantispidae, the eggs are laid on stalks (Fig. 34.6), but most other families attach the eggs directly. In Sisyridae there may be a light, silken covering, but females of other families leave the eggs naked.

Three larval instars occur in most families, and there are very few reports of larger numbers—5 in *Ithone fusca* (Tillyard 1922a), 4 in a few Coniopterygidae. Up to 12 instars have been noted for an American dilarid but this may have been due to unnatural rearing conditions.

Larvae are diverse in form and habits. Most are active predators, but the subterranean ithonid larvae apparently



Fig. 34.6 Eggs of *Nymphes myrmeleonides*, Nymphidae. [D. J. Lee]

feed from decaying plant material (Gallard 1932). Second and 3rd instar larvae of Mantispidae are 'grub-like' parasites in the egg sacs of various spiders and in the nests of social Hymenoptera. The only berothid (a Nearctic *Lomamyia*) of which the full life cycle is known is a termitophile and has grub-like 2nd instar larvae. Sisyrid larvae use their extremely long, thin jaws as obligate feeders on fresh water sponges, and perhaps occasionally bryozoans. The older instars of sisyrids have ventral abdominal gills, the only lacewing larvae to do so. Elongate osmylid larvae, also with long needle-like jaws, occur either in damp situations near streams or under bark, a habitat shared with Psychopsidae and some Berothidae. Coniopterygid, hemerobiid and chrysopid larvae occur widely on vegetation. Myrmeleontoid larvae occur in litter or on the bark of trees, and are often extremely well camouflaged. Larvae of *Osmylops* and *Myiodactylus* are flattened and disc-like and occur among foliage, where they lie in wait with their jaws open at more than 180°. Most myrmeleontid larvae occur in sandy soil (see pp. 91–92).

The cocoon is spun of silk secreted by the Malpighian tubules and spun through the anus. The pharate adult often emerges completely from the cocoon before eclosion.

Natural Enemies. Neuroptera are attacked by representatives of all the major groups of parasitic Hymeno-

ptera, and some parasites appear to be very host specific. Heloridae and anacharidine figitids attack Chrysopidae and Hemerobiidae respectively in many parts of the world. The most common stages attacked are larvae and prepupae within the cocoons but egg, pupal and (rarely) adult parasites are also known.

A wide range of arthropod predators feed casually on Neuroptera, and some (such as larvae of particular clerid beetles feeding in chrysopid cocoons) may be more specific. Adult chrysopids and antlions have been noted among the prey of Australian *Bembix* wasps. Crepuscular and nocturnal species are preyed upon by bats, and some chrysopids have a remarkable, defensive 'dropping' behaviour to counter this (L. A. Miller 1984). Aggregations of ithonids may be attacked by currawongs and other insectivorous birds, as well as by spiders, large ants and frogs.

Economic Significance. As predators, Neuroptera are generally beneficial. Hemerobiidae, Chrysopidae and Coniopterygidae, in particular, feed on a wide range of small, sap-sucking, arthropod pests (such as psyllids, aphids, scale insects and mites) and lepidopteran eggs and larvae, and have been considered for biological control work in many parts of the world. Chrysopids can sometimes be attracted to field crops by yeast hydrolysate sprays or be mass-reared for release. Many Hemerobiidae appear to have very low developmental temperature thresholds, so that they are among the few predators active on crops early in spring.

The economic importance of other families is slight. Although ithonids have been used in attempts to control pest species of scarabaeid larvae, this appears to have been based on the false assumption that they naturally feed on such larvae. Adult ithonids are occasional 'nuisances', as aggregations may enter houses. As with many other aquatic insects, sisyrids and neurorthids may indicate water quality as they (and the sponge prey of Sisyridae) are at times highly susceptible to pollution.

Special Features of the Australian Fauna

Australian Neuroptera include many of the more archaic groups and some higher taxa scarcely found elsewhere in the world. Although some genera of many families are globally widespread, endemism at both generic and specific levels is very high and well over 90% of Australian species are not known from outside the country. The northern fauna sometimes has affinities with that of New Guinea, and some elements of the Bassian fauna are related to taxa in South America. Four small families appear to be absent from Australia: Brucheiseridae, with 2 small South American species; Rapismatidae, a primitive group formerly allied with Ithonidae, are montane Oriental; Dilaridae are Holarctic, Neotropical and Afrotropical; and Polystoechotidae occur in both North and South America.

Nymphidae (which are thought to represent the line of development leading to the higher Myrmeleontoidea) occur only in Australia, Lord Howe I. and New Guinea, with an early, unconfirmed record from the Philippines, and Psychopsidae are otherwise known from southern

Africa and the Oriental Region. Ithonidae are almost entirely Australian. Myrmeleontidae: Stilbopteryginae (earlier considered as part of a distinct family, Stilbopterygidae) occur only in Australia. Two of the primitive genera of Chrysopidae: Nothochrysinae occur in south-eastern Australia, and the Osmylidae are diverse, with some subfamilies shared only with South America and New Zealand.

As a result of recent revisionary studies, adults of the Australian Neuroptera are now tolerably well known, although undoubtedly many further species await description. Many families are widely distributed in Australia

but, in general, Myrmeleontidae and Ascalaphidae are most abundant in the drier regions. The Myrmeleontidae: Dendroleontini are a predominantly Australian radiation with relatively few species elsewhere. Some other families (Psychopsidae, Nymphidae, Coniopterygidae) are most diverse in the east and south-east and Osmylidae are particularly characteristic of subalpine areas with a few species being found above the treeline. The fauna of Tas. is relatively impoverished but at least 9 families are present with species representing both widespread taxa and the eastern Bassian fauna. The only possible Tasmanian endemics are some Osmylidae and Chrysopidae.

CLASSIFICATION

Order NEUROPTERA (623 Australian spp.)

Uncertain Affinity (0)
Rapismatidae (0)
Brucheiseridae (0)

CONIOPTERYGOIDEA (50)

1. Coniopterygidae (50)

ITHONOIDEA (14)

2. Ithonidae (14)

OSMYLOIDEA (58)

3. Osmylidae (40)
Dilaridae (0)
4. Neurorthidae (2)
5. Sisyridae (16)

MANTISPOIDEA (75)

6. Berothidae (30)
7. Mantispidae (45)

HEMEROBIOIDEA (102)

8. Hemerobiidae (35)
9. Chrysopidae (55)
Polystoechotidae (0)
10. Psychopsidae (13)

MYRMELEONTOIDEA (323)

11. Nymphidae (23)
12. Myrmeleontidae (250)
13. Ascalaphidae (40)
14. Nemopteridae (10)

The groupings of families adopted here reflect recent opinions, but the higher classification of the Neuroptera is by no means clear. It seems that the Coniopterygidae and Ithonidae are both ancient groups which became phylogenetically isolated early in the history of the order. Hemerobioidea are also relatively well defined other than for the inclusion of Psychopsidae, but the relationships between the remaining families are more obscure:

whether or not the Berothidae and Mantispidae should comprise a distinct superfamily is debatable, as is the composition of the Osmyoidea and the derivation of all superfamilies. Likewise, intra-family groupings are often not wholly satisfactory—in the Myrmeleontidae, for example, Acanthaclisinae are sometimes considered to be a tribe of Myrmeleontinae.

Key to the Families of Neuroptera Known in Australia

The family keys do not include superfamily groupings. They are designed for simple, practical use, and should not be used for implications on phylogeny or for the non-Australian fauna.

ADULTS

1. Very small insects, fore wing length to about 5 mm; wings and much of body covered with waxy, mealy secretion; costal area with, at most, 1 or 2 (basal) cross-veins (Fig. 34.7E) **Coniopterygidae**
Not as above (larger, not waxy, costal area with more numerous cross-veins) 2
- 2(1). Fore wing and hind wing of markedly different shape: hind wing greatly elongate (Fig. 34.8G), thread-like or expanded near apex **Nemopteridae**
Fore wing and hind wing of generally similar shape 3
- 3(2). Fore legs raptorial, femur strongly thickened; prothorax greatly elongate (Fig. 34.3D) **Mantispidae**
Fore legs not raptorial; other features not as above 4
- 4(3). Antennae filiform or moniliform, never clubbed or with apex broadened—if thickened, this occurs over most of flagellum and is uniform 5
Antennae with distinct apical club, or apex thickened 13
- 5(4). Very stout-bodied, with hind wing very broad near base (Figs 34.2F, 7A) (appearance 'moth-like') **Ithonidae**
Not as above: if, rarely, body stout, hind wing no broader than fore wing near base 6
- 6(5). Ocelli present, at least represented by raised tubercles on vertex **Osmylidae**
Ocelli absent 7
- 7(6). Vena triplica present (i.e. Sc, R₁ and Rs equispaced and parallel, with Sc and R₁ not converging distally) (Fig. 34.8D) **Psychopsidae**

- Not as above..... 8
- 8(7). Sc and R₁ fused apically and thence curved posteriad to enter margin at or beyond wing apex (Figs 34.8E, F) **Nymphidae**
- Sc and R₁ connected by a cross-vein towards apex, if fused entering margin well before wing apex 9
- 9(8). Fore wing with at least 2 apparent Rs veins arising from R (Fig. 34.8A) **Hemerobiidae**
- Fore wing with only a single Rs, arising from R near the base 10
- 10(9). Hind wing with numerous cross-veins between R₁ and Rs (Fig. 34.1) (medium to large, generally green species) **Chrysopidae**
- Hind wing with only a few (2 or 3) cross-veins between R₁ and Rs 11
- 11(10). Fore wing costal cross-veins simple (Fig. 34.7G); wings not hairy (usually very small, fore wing to about 6 mm) **Sisyridae**
- Fore wing with at least some costal cross-veins forked 12
- 12(11). Fore wing with several Sc–R₁ cross-veins (Fig. 34.7C); wings not hairy (usually very small, fore wing to about 7 mm) **Neurorthidae**
- Fore wing with only basal Sc–R₁ cross-vein (Fig. 34.7F), very rarely a second cross-vein beyond half length of wing; wings often densely hairy or with thickened, scale-like hairs on veins (usually larger than above) **Berothidae**
- 13(4). Antennae longer than half fore wing length, strongly clubbed (Fig. 34.2D) **Ascalaphidae**
- Antennae short, usually much shorter than half fore wing length, more or less clubbed or expanded at apex (Fig. 34.2B) **Myrmeleontidae**

LATE INSTAR LARVAE

Larvae of most Australian species are unknown, and key characters could thus occasionally prove invalid. First instar larvae sometimes differ substantially from later stages, and are not included.

1. Labial palps absent; abdominal segments with paired ventral gills (Figs 34.10C, D) (aquatic) **Sisyridae**
- Labial palps present; no ventral gills (usually terrestrial) 2
- 2(1). Very small (2–3 mm); labial palp 2-segmented, with apical segment enlarged; antenna 2-segmented (Fig. 34.9) **Coniopterygidae**
- Usually larger; labial palp and antenna both with more than 2 segments 3
- 3(2). Mandible with large internal preapical tooth or teeth 4
- Mandible without large internal preapical tooth or teeth; occasionally with small papillae, which then occur also elsewhere on the mandible 6
- 4(3). Mandible with 1 preapical tooth (Figs 34.12F, G); hind tibia and tarsus not fused **Nymphidae**
- Mandible with more than 1 (usually 3) preapical teeth; hind tibia and tarsus usually fused 5
- 5(4). Lateral body processes well developed, usually 2 each on mesothorax and metathorax and 1 on each of at least first 7 abdominal segments; hind margin of head usually strongly bilobed; hind tarsal claws normal (Fig. 34.12D) **Ascalaphidae**
- Lateral body processes weakly developed or, often, virtually absent, at least on abdomen; hind margin of head usually not bilobed; hind tarsal claws flexed forwards and enlarged (Fig. 34.12C) **Myrmeleontidae**
- 6(3). Either 'neck' elongate, with prothorax considerably longer than broad and very narrow or anterior region of prothorax inconspicuous; mandible with several papillae along inner edge (Fig. 34.12A) **Nemopteridae**
- Not as above 7
- 7(6). Body scarabaeiform (Fig. 34.10G); tibiae and tarsi fused; eyes absent **Ithonidae**
- Body generally not scarabaeiform; tibiae and tarsi separate; eyes present 8
- 8(7). Tarsi with 1 claw; mandibles short (Figs 34.11C, D) (parasitic in spider egg sacs) **Mantispidae**
- Tarsi with 2 claws; mandibles long (free living) 9
- 9(8). Mandible and maxilla inwardly curved from base 10
- Mandible and maxilla straight, usually long and slender, rarely inwardly curved at apex 12
- 10(9). Labial palp 5-segmented; antenna 10-segmented; frons tapered anteriorly; dorsal surface of abdomen bare (Fig. 34.12B) **Psychopsidae**
- Labial palp with more than 5 segments, or segmentation very indistinct; antenna with 1 segment very long, usually with secondary irregular annulation giving impression of large number of ill-defined segments 11
- 11(10). Empodium trumpet shaped; abdomen and thorax often with long hairs (Figs 34.11F–H) (may carry debris) **Chrysopidae**
- Empodium not trumpet shaped (except in 1st instar); abdomen and thorax with short hairs, sometimes appearing bare (Fig. 34.11E) (never carry debris) **Hemerobiidae**
- 12(9). Mandible and maxilla incurved at apex (Figs 34.11A, B) (aquatic) **Neurorthidae**
- Mandible and maxilla straight 13
- 13(12). Maxilla base broader than mandible base (Figs 34.10A, B); antenna 5-segmented **Berothidae**
- Maxilla base of similar width to mandible base (Figs 34.10E, F); antenna multisegmented **Osmylidae**

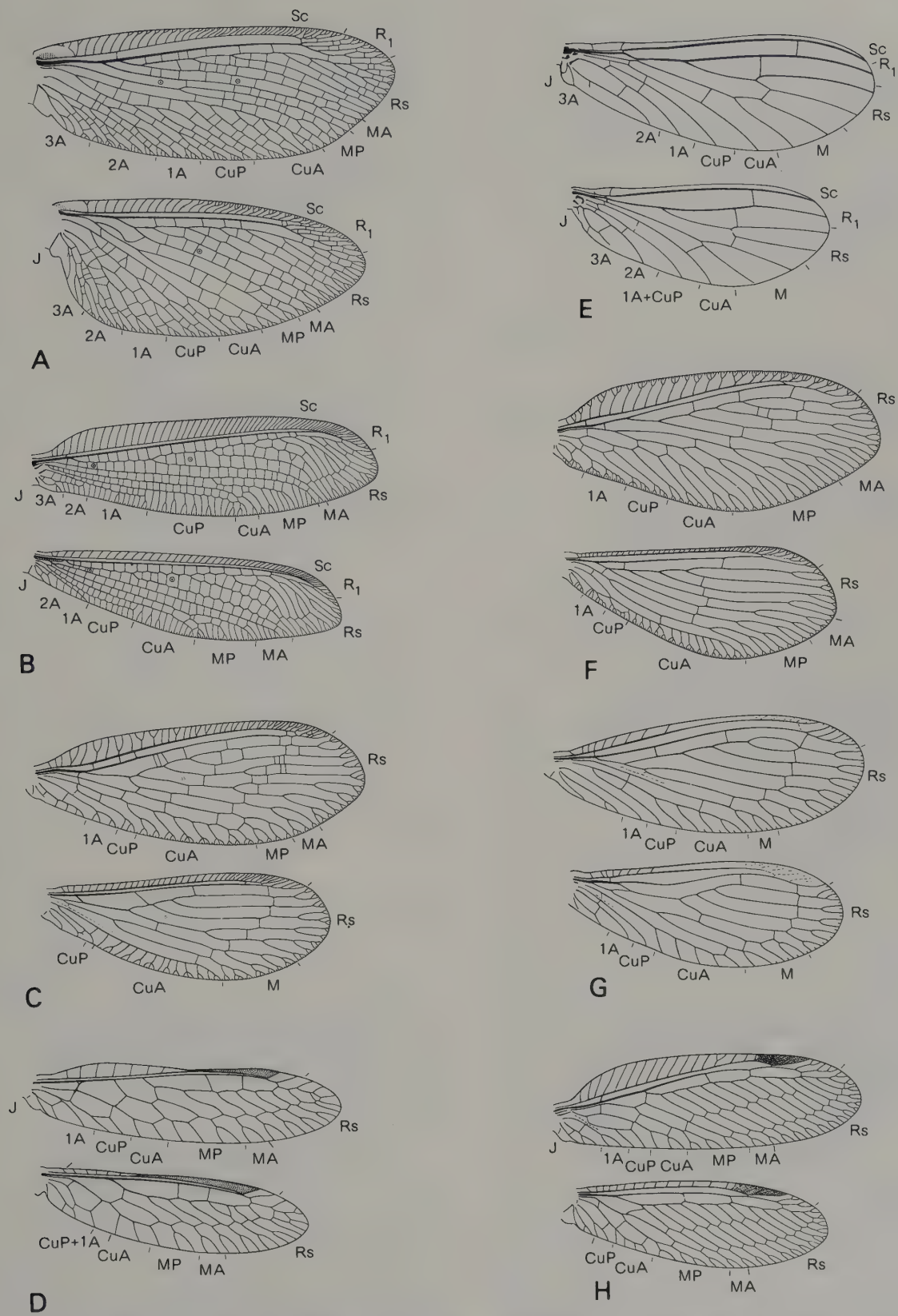


Fig. 34.7 Wings: A, *Ithone* sp., Ithonidae; B, *Eidoporis* sp., Osmylidae; C, *Austroneurorthus* sp., Neurorthidae; D, *Campion* sp., Mantispidae; E, *Neosemidalis* sp., Coniopterygidae; F, *Spermophorella* sp., Berothidae; G, *Sisyra* sp., Sisyridae; H, *Ditaxis* sp., Mantispidae. [M. Quick]

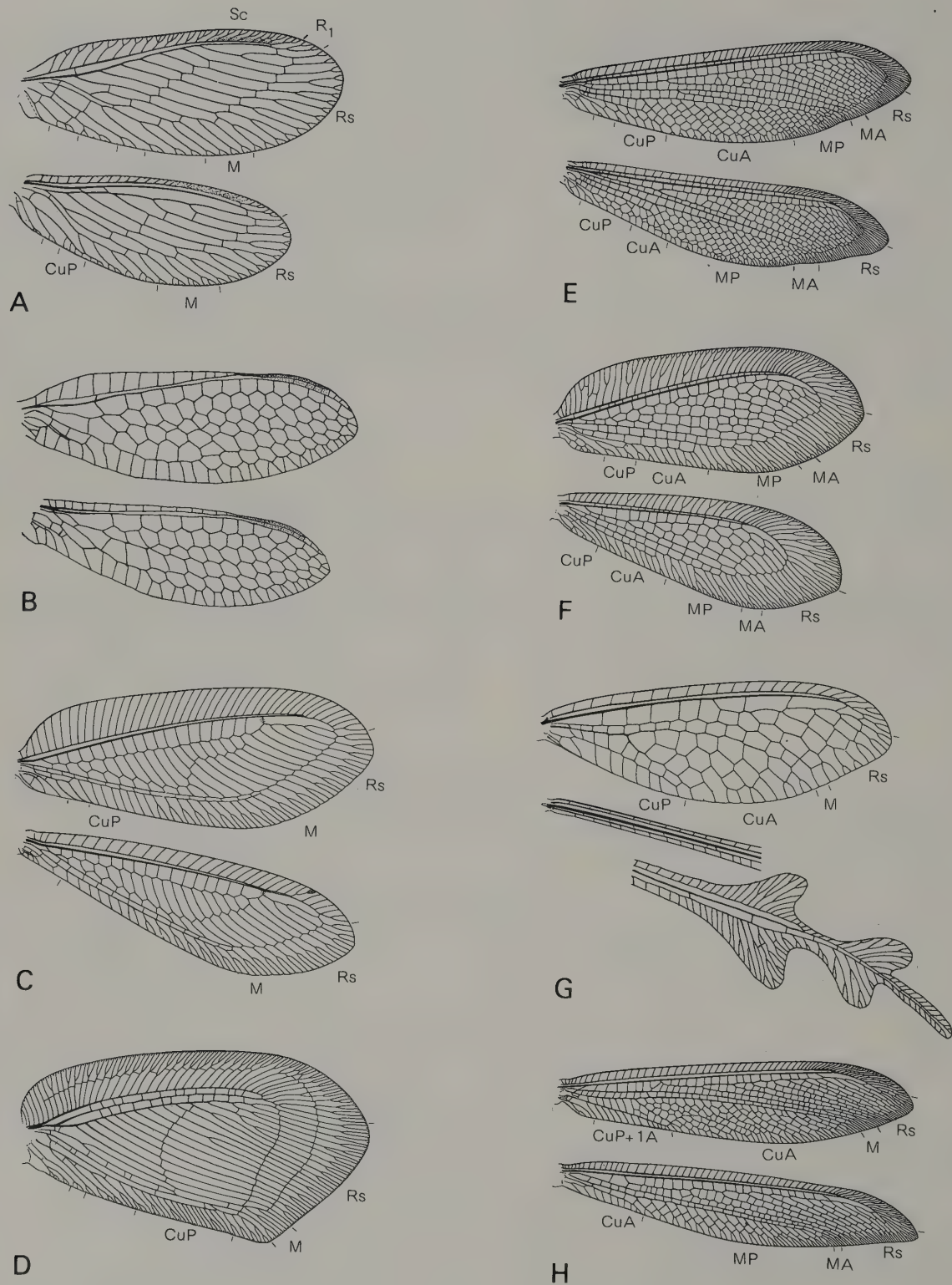


Fig. 34.8 Wings: A, *Psychobiella* sp., Hemerobiidae; B, *Dictyochrysa* sp., Chrysopidae; C, *Oligochrysa* sp., Chrysopidae; D, *Psychopsis* sp., fore wing, Psychopsidae; E, *Nymphes* sp., Nymphidae; F, *Myiodactylus* sp., Nymphidae; G, *Chasmoptera* sp., Nemopteridae; H, *Distoleon* sp., Myrmeleontidae.

[M. Quick]

Superfamily CONIOPTERYGOIDEA

A very isolated group of Neuroptera, with many very distinctive features. One family only is generally recognised. Coniopterygidae have a very reduced venation (Fig. 34.7E) with at most 1 or 2 costal cross-veins. There is no trace of a pterostigma, and the distinctive wing coupling involves hamuli at the base of both wings. The genitalia are also distinctive: the male has an aedeagus, and the female genitalia are rather uniform. A spermatophore is not deposited, again differing from most other Neuroptera. Larvae have only 6 Malpighian tubules rather than the 8 characteristic of other families.

1. Coniopterygidae (dusty-wings). Very small species, with fore wing length usually less than 6 mm. Some species with fore wing length 2–3 mm are by far the smallest Neuroptera. Body, wings and appendages usually with white or grey wax or 'meal' secreted by wax glands on various parts of the body, so that the insects superficially resemble whitefly (HEMI: Aleyrodidae). Antennae short and moniliform; scape enlarged; pedicel elongate; the number and form of segments can be of taxonomic value and the basal 3 segments are enlarged in many males. Ocelli absent. Wings generally longer than body, rarely shorter or with hind wing reduced, sometimes with distinct dark grey or black spotting, apex rounded; Rs 2-branched; wings held in steep 'tent' over body when at rest.

Mainly arboreal. Adults are often beaten from trees, and may also be attracted to light. The oval eggs are laid singly on foliage or bark, and hatch in 1–3 weeks. Larvae take a few weeks to a few months to develop; the biology of only one Australian species, *Cryptosceneae australiensis*, is known in any detail (Kimmins and Wise 1962). Flat, silken cocoons, often with two distinct envelopes, are spun on vegetation, and the prepupa is the major overwintering stage for many temperate region species. Larvae (Fig. 34.9) are short and fusiform, with the head and mouth-parts short; the jaws are almost straight, and needle-like.

The family occurs in all regions, although many genera and species groups are geographically highly restricted. Two subfamilies are recognised:

Fore wing with 1 R–M cross-vein in centre of wing; hind wing vein Rs not branching from R very near base of wing. Larval antenna about twice as long as labial palp
..... CONIOPTERYGINAE

Fore wing with 2 R–M cross-veins near centre of wing; hind wing vein Rs branching from R very near wing base. Larval antenna about as long as labial palp
..... ALEUOPTERYGINAE

Australian CONIOPTERYGINAE include *Coniopteryx* (9 spp.) and *Neosemidalis* (16 spp.). The latter is apparently an Australian endemic genus, and *Coniopteryx* is world-wide. Australian ALEUOPTERYGINAE are dominated by *Heteroconis* (12 spp.) which occurs throughout the Oriental region, and also include *Cryptosceneae* (4 spp.) and *Spiloconis* (1 sp.). Both the latter genera occur in New Guinea and the Oriental region, and one species of *Cryptosceneae* is shared with New Zealand. Most

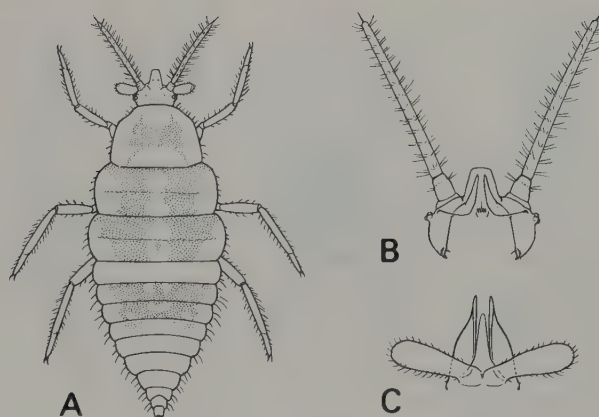


Fig. 34.9 Coniopterygid larva: A, dorsal; B, head, ventral, maxillae and labium removed; C, maxillae and labium, ventral. [M. Quick]

Australian species were included in a world-wide revision of the family by Meinander (1972).

Superfamily ITHONOIDEA

A primitive and isolated group of Neuroptera, at one time treated as a distinct suborder. The Oriental Rapismatidae formerly were included in the Ithonidae, but are clearly distinct (Barnard 1981).

2. Ithonidae (moth lacewings). A small, archaic family almost wholly restricted to Australia. Adults (Fig. 34.2F) are stout, with broad wings (fore wing length 25–30 mm), and superficially resemble some small hepialid moths. Most species have uniformly greyish brown wings, but those of *Varnia* are patterned. Venation (Fig. 34.7A) is complex and nygmata are present. Genitalia of both sexes are distinctive: males have greatly enlarged claspers, and the female ovipositor (used for laying eggs in sandy soil) has been likened to a ploughshare. The large (1.7 mm) eggs are laid singly and hatch in about a month in *Ithone fusca*. The life cycle of this species lasts two years, and the larva is subterranean. It (Figs 34.10G, H) is pale, blind and scarabaeiform, with short straight jaws, and is unusual in Neuroptera in feeding on partially decayed plant material. Adults often swarm, with enormous numbers participating in crepuscular or nocturnal mating flights and concealing themselves in crevices during the day.

Other than the North American *Oliarces*, the family occurs only in Australia. The 3 genera (Riek 1974b) are *Ithone* (10 spp.), predominantly found in sandy coastal areas, *Megalithone* (2 spp.) from higher altitude areas of southern Qld and N.S.W., and *Varnia* (2 spp.) with a considerable inland range in semi-arid Australia.

Superfamily OSMYLOIDEA

The integrity of this superfamily is doubtful, and the families included here are structurally diverse. Sisyridae and Neurorthidae are often associated with water, as are many Osmylidae; others occur in open forest. Osmylidae are the only Neuroptera with ocelli.

3. Osmylidae. A diverse group of lacewings, united by having 3 ocelli which, however, are not always very distinct. Generally medium to large insects (fore wing length

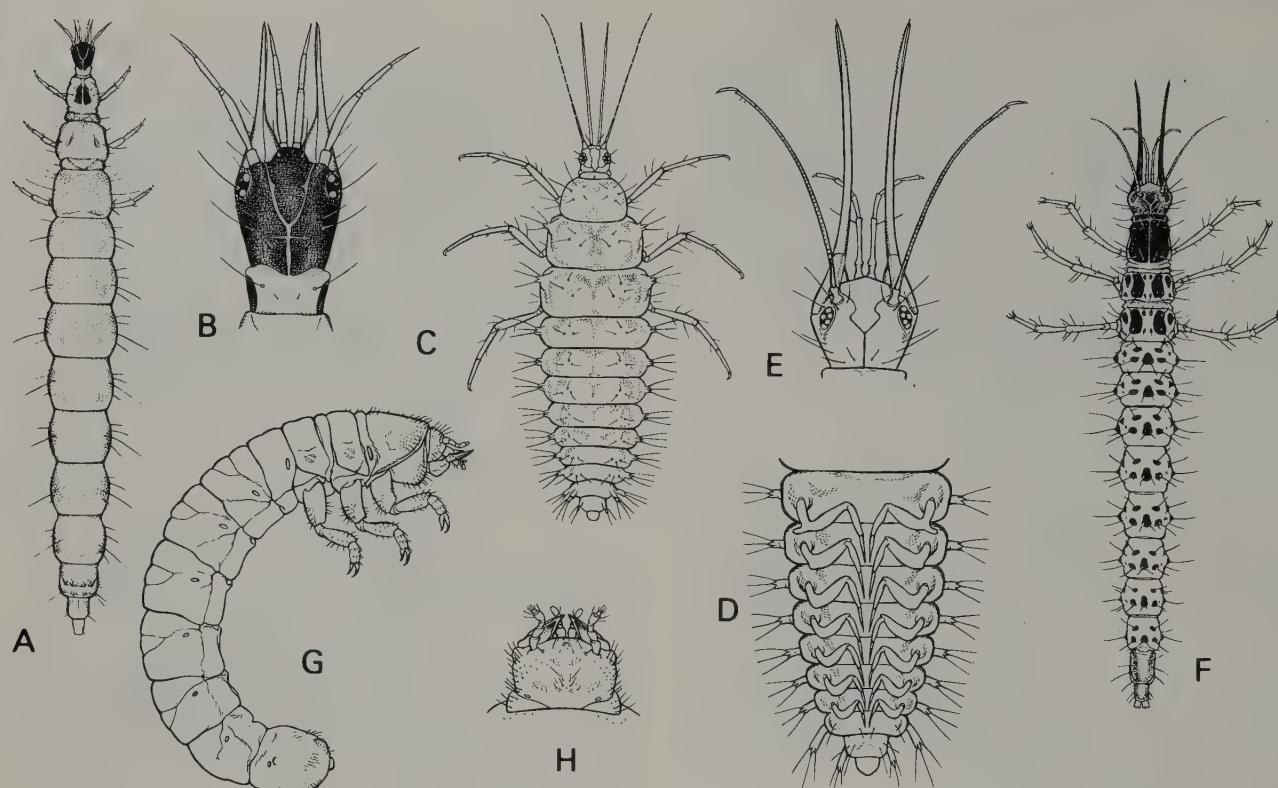


Fig. 34.10 Larvae: A, B, berothid, dorsal and head enlarged; C, D, *Sisyra* sp., Sisyridae, whole larva, dorsal and abdomen, ventral; E, F, *Kempynus* sp., Osmylidae, head enlarged and dorsal; G, H, *Ithone* sp., lateral, and head, dorsal, Ithonidae.
[M. Quick]

12–30 mm or more), with the wings (Fig. 34.7B) often patterned with grey or brown and rather broad. The antennae are usually less than half as long as the fore wing. The female genitalia are typified by an enlarged gonocoxite 9, and 2 spermathecae.

The biology of most species is unknown, but some subfamilies occur predominantly near streams, and others in drier open forest. Eggs are laid in short rows (of up to 12) on vegetation, tree trunks or stones, and the larvae (Figs 34.10E, F) are long and fusiform, with long tapering straight jaws. They feed on a variety of insects, and the more aquatic ones are believed to probe in mud for larvae of Chironomidae (DIPT). Most species appear to be univoltine, with adults appearing in summer or autumn.

The family occurs over much of the world, but apparently is absent from North America. Australian species have been treated by Kimmins (1940) and New (1983a, b; 1986a, b). Five subfamilies are represented but only 2 are diverse.

Key to the Subfamilies of Osmylidae Known in Australia

1. Fore wing vein MP forks near base of wing, usually between separations of MA and first branch of Rs from Rs, sometimes opposite separation of MA ... 2
Fore wing vein MP forks more distally, usually beyond half wing length 3
- 2(1). Wings broad, not falcate, with relatively few cross-veins; sometimes with embossed spot on hind margin of fore wing; relatively small, fore wing length 17–20 mm (northern Australia) *SPILOSMYLINAE*

Wings usually long and somewhat falcate, with numerous cross-veins; never with embossed spot on hind margin of fore wing; relatively large, fore wing length 24–37 mm (predominantly south-eastern Australia) *KEMPYNINAE*

- 3(1). Both wings with many subcostal cross-veins *PORISMINAE*
Wings with basal subcostal cross-vein only 4
- 4(3). Veins Rs and MA in both wings separate near wing base *STENOSMYLINAE*
Veins Rs and MA in both wings separate about one third wing length from base *EIDOPORISMINAE*

SPILOSMYLINAE are represented by 2 tropical species of the widespread *Spilosmylus*; the genus is much more diverse in New Guinea. The embossed spot on the hind margin of the fore wing distinguishes the more common species from all other Australian osmylids, and it is bright green in life.

EIDOPORISMINAE (1 sp.) is an endemic subfamily with *Eidoporis pulchellus* known from N.S.W. and southern Qld. It has distinctive venation. The sole species of *PORISMINAE*, *Porismus strigatus* (Fig. 34.2E), is one of the most brightly coloured osmylids, being steel-blue to black with lemon-yellow markings, and parts of the body reddish brown. It is not uncommon in drier eucalypt forests in the south-east, where larvae live under bark.

STENOSMYLINAE (about 20 spp.) are the most diverse Australian osmylids, and occur also in South America. *Euporis albatrox* has dark steel-blue patterned wings,

and some species of *Oedosmylus* are attractively mottled with brown. *Stenosmylus*, with long narrow wings, is sometimes common. *Carinosmylus* has spectacularly developed female genitalia, including a ventral keel. *Stenolysmus* is rather similar to the last 2 genera in venation, and the 3 genera seem to be a relatively advanced group in the subfamily. The terrestrial larvae live under bark.

The KEMPYNINAE, another southern group, shared with New Zealand and temperate South America, are found predominantly near water in the south-east, sometimes at relatively high altitudes, and include our largest osmylids. Adults sometimes cluster on rocks and tree trunks near streams, and larvae have been found under stones and in litter beside streams. The 3 Australian genera are *Kempynus* (8 spp.; also in New Zealand), *Australysmus* (4 spp.) and *Clydosmylus* (1 sp.).

4. Neurorthidae. Formerly placed in the Sisyridae, but recognised as a distinct family by Zwick (1967). The small (fore wing length to about 7 mm), delicate adults differ from those of sisyrids by having some fore wing costal cross-veins forked, and by usually having distinct nygmata (Fig. 34.7C). Generally adults have been found in damp habitats, often bordering streams and in dense forests. Larvae occur in fast-flowing streams and in moist litter.

The 3 small genera, one each in the western Palaearctic region, Asia and Australia, are very similar, and the aquatic larva of *Austroneurorthus* from south-eastern

Australia (Figs 34.11A, B) is almost indistinguishable from that of the European *Neurorthus*.

5. Sisyridae (sponge-flies). Small (fore wing length 4–6 mm) lacewings, similar to Neurorthidae and differing as above. Also resemble small Hemerobiidae but differ in having only one Rs from R in the fore wing (Fig. 34.7G). Antennae moniliform. Adults occur near water, and lay massed eggs on vegetation overhanging water; the eggs are unusual in being covered with silk. Larvae (Figs 34.10C, D) drop to the water and swim by flexing the body until they find a freshwater sponge, on which they are specialised predators. The long straight jaws are used, often only one at a time, to probe the sponge tissue and extract the contents. The last larval instar pupates well away from water, and the pupa may overwinter in the silken cocoon. Most species appear to be univoltine. Sisyridae are widely distributed, and 2 genera are recorded from Australia. *Sisyra* (8 spp.) is cosmopolitan and *Sisyra* (2 spp.) occurs also in Africa, India and possibly elsewhere in the Orient.

Superfamily MANTISPOIDEA

Contains 2 families which lack fore wing nygmata and have few cross-veins between R_1 and Rs. Mantispidae have raptorial fore legs, a feature shared with some non-Australian Berothidae. Berothidae have conspicuously hairy wings, which are sometimes narrow and strap-like. The close relationship between these families is emphasised by MacLeod and Adams (1968).

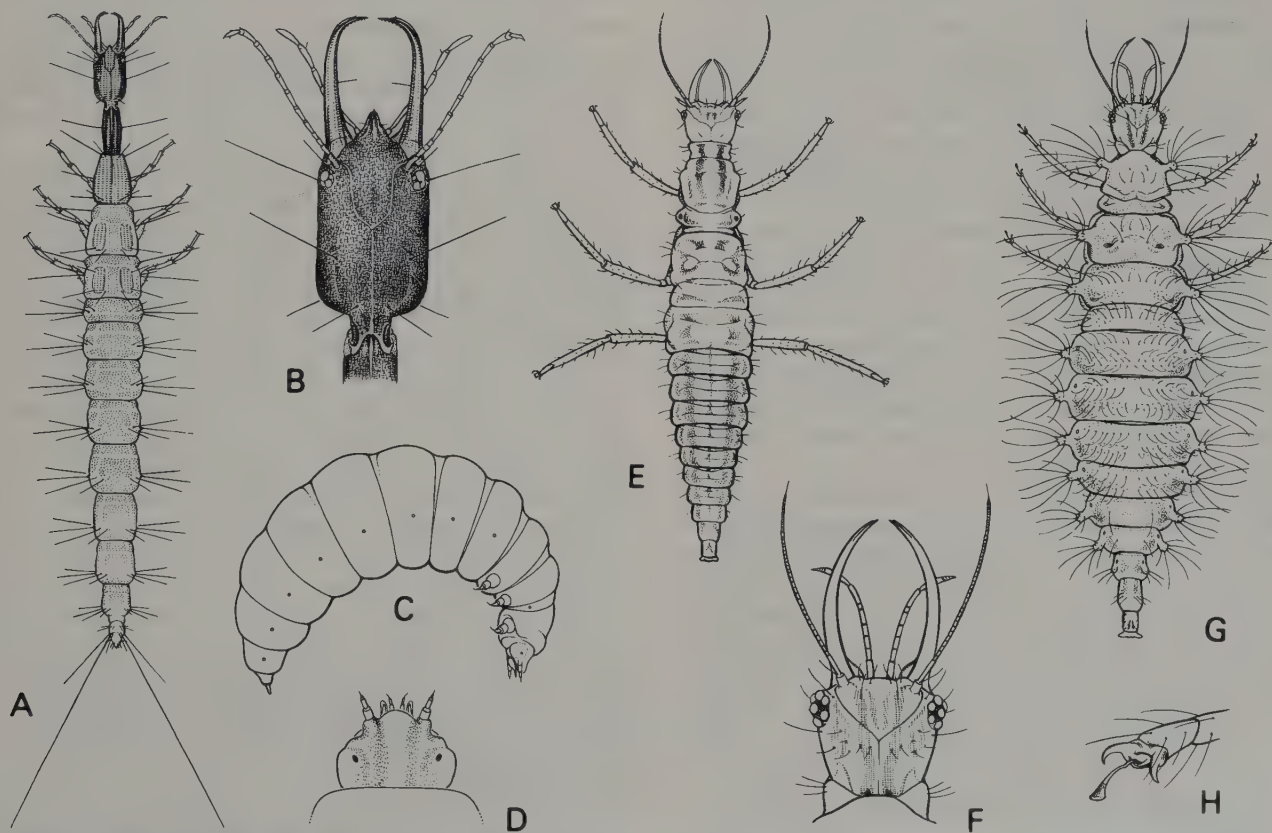


Fig. 34.11 Larvae: A, B, neurorthid, dorsal and head enlarged; C, D, *Mantispa* sp., Mantispidae, 3rd instar, lateral, and head enlarged, dorsal; E, hemerobiid, dorsal; F–H, *Chrysopa* sp., Chrysopidae, head enlarged, dorsal, apex of leg.

[M. Quick, T. Binder]

6. Berothidae. Small to medium-sized lacewings (fore wing length 6–15 mm). Antennae shorter than fore wing, usually setose and with scape enlarged. Wings (Fig. 34.7F) subequal, shape variable: rounded, strap-like or (rarely) falcate; usually with veins strongly setose and females of some species and males of a few have specialised scale-like hairs (e.g. *Spermophorella*) which may also be present on the pronotum or coxa of the fore leg or on the abdomen. The females may have a pair of long filamentous processes ('hypocaudae') on the gonocoxite.

Life histories are not known with any certainty. Larvae of a North American species feed on termites, which they chemically immobilise. In Australia, biological knowledge is limited to *Spermophorella*, females of which lay batched, stalked eggs, and the larvae (Figs 34.10A, B) of which occur under bark. They have straight mouth-parts, and are distinguishable from other neuropteran larvae by the very broad maxilla base.

Berothidae are widely distributed, and all Australian species (representing about 6 genera), belong to the Berothinae, one of the 4 subfamilies (Aspöck and Aspöck 1984, 1985, 1986). Many species appear to be limited to drier areas, and the most diverse genera are the broad-winged *Spermophorella* and the narrow-winged *Stenobiella*. The falcate-winged *Isoscelipteron* with a species in Qld has the widest known distribution of any berothid genus (southern Europe, northern Africa, Asia, Australia).

7. Mantispidae. Very distinctive mantid-like lacewings; small to medium sized (fore wing length 5–25 mm); strongly raptorial fore leg (Fig. 34.3D) with elongate coxa; pronotum long. Wings (Figs 34.7D, H) narrow, with a very clearly defined pterostigma. Antennae short, sometimes weakly (e.g. *Campion*) or conspicuously (*Euclimacia*) thickened. Some species are brightly coloured and appear to mimic social Hymenoptera as the adults tend to be diurnal and are sometimes found on flowers. Other species are nocturnal or crepuscular.

Lambkin (1986a, b) recognised 45 Australian species, in the subfamilies MANTISPINAE, CALOMANTISPINAE and DREPANICINAE which have a 5-segmented tarsus and in which the ovipositor is not strongly produced. Symphrasinae are limited to the New World, and their larvae are sedentary, generalist predators most commonly found in nests of social Hymenoptera (especially Vespidae) and burrows of scarab beetle larvae. Mantispines are specialised, obligate parasites of spiders and the triungulin 1st instar larva either boards a female spider and enters the egg sac as it is produced, to feed on the eggs, or searches directly for an egg sac. Later instars (Figs 34.11C, D) are relatively immobile. The pattern of attack appears to be constant in some mantispines, and variable in others. Some species, at least, are able to retard development of their hosts through chemical interference. Pupation occurs within the host egg sac.

Little is recorded on the biology of Australian taxa, but *Campion australasiae* females may congregate on trees or telegraph poles to lay their many hundreds of small ovoid eggs on short stalks (McKeown and Mincham 1948). In common with many other specialised, parasitic insects

with potentially high mortality in an early stage, fecundity is very high, and up to several thousand eggs may be laid by a single female, with individual batches comprising several hundred eggs.

The family is widely distributed, especially in warmer parts of the world. The most diverse genus in Australia is the endemic *Theristria* (23 spp.).

Superfamily HEMEROBIOIDEA

The families included here comprise the Hemerobiidae and the Chrysopidae which include valuable predators of crop pests (New 1975), and an archaic, economically less important group (Psychopsidae). The fore wing of Hemerobiidae has 2 or more stems of Rs directly from R (as Rs is assumed to be fused with R), and the veins of Chrysopidae are often strongly angled. Venation of Psychopsidae, which have very broad wings, is denser and more complex.

8. Hemerobiidae (brown lacewings). Small, delicate, often pale species, with fore wing length 5–12 mm. Antennal scape usually enlarged and moniliform antennae often nearly as long as fore wing. Wings (Fig. 34.8A) usually subequal but some species of *Notiobiella* have the hind wing reduced. Several non-Australian hemerobiids have it reduced to a small stub, and the fore wing short and thickened: such species are undoubtedly flightless. A Holarctic species, *Psectra diptera*, is dimorphic, with the wings either normal or considerably shortened. A frenulum type of wing coupling is normally present in macropterous forms, and the presence or absence of a recurrent humeral vein in the fore wing separates two groups of genera. When that vein is present the wings are usually broad and held relatively flat when the insect is at rest. When it is absent, wings are long and narrow and held vertically. Trichosors are usually distinct.

Adults are found most commonly on trees and shrubs, but a few species are more characteristic of low vegetation. All are predators, and are typically very cryptic insects: many drop and feign death if disturbed. They may live for several months, during which females lay up to several hundred elongate eggs attached by their sides to vegetation (up to about 2500 eggs have been recorded in a non-Australian species). The chorion is often lightly sculptured, and eggs may hatch in a few days or overwinter. The fusiform larvae (Fig. 34.11E) are active predators, and do not carry debris. They usually have only short body hairs, and the head in some is retracted into the thorax. Hemerobiid larvae differ from those of Chrysopidae by having the tarsal empodium trumpet-shaped only in the 1st instar. The apex of the abdomen, as in some other arboreal lacewing families, is used to 'hold on' during locomotion. The larval period is several weeks, and the prepupa and pupa occur in a (usually) loosely woven silk cocoon on vegetation or under bark. This is the major overwintering stage in northern temperate species. Many of those undergo 1–3 relatively discrete generations each year.

The family is of world-wide distribution. Australian species (New 1988a) represent about 12 genera, and appear to be most numerous in the east. Many species are

rare, and only 2 can be regarded as generally common. The slender-winged *Micromus tasmaniae* is abundant, especially throughout the temperate parts of the country, and often feeds on aphids on cereals or other crops. *Drepanacra binocula* (Fig. 34.2c) has broad, slightly falcate fore wings which are very variable in pattern. Both species occur also in New Zealand, but most other Australian species are apparently endemic or shared with New Guinea. *Carobius* (9 spp.) contains several attractively mottled species; *Notiobiella* (4 spp.) contains broad-winged forms and one of the few green hemerobiids (*Notiobiella viridis*). Some *Zachobiella* (3 spp.) are minute and narrow-winged. The otherwise widespread *Hemerobius* is represented in Australia by only one rare species.

9. Chrysopidae (green lacewings). One of the largest families of Neuroptera, with about 2000 named species, and very widely distributed. Many aspects of the family are discussed in Canard *et al.* (1984). The species are predominantly green and delicate, with fore wing length of 8–30 mm. Most have the wings clear and 'glassy' but some are brightly patterned or spotted. In one Australian genus (*Oligochrysa*) veins Sc and R₁ fuse near the wing apex (Fig. 34.8c), but in all other Australian species these veins are linked by short distal cross-veins. The venation is distinctive with some longitudinal veins closely associated, to form a 'pseudomedia' (Psm) and 'pseudocubitus' (Psc), and distinct irregular 'cellules' in both wings. Trichosors are absent and the fore wing jugal lobe is usually reduced.

Recent forms are placed in 3 subfamilies, all represented in Australia (New 1980, 1983c). Fossil forms make up the Mesochrysopinae (= Mesochrysopidae of p. 175).

Key to the Subfamilies of Chrysopidae Known in Australia

1. Both basal subcostal cross-vein and intramedian cell absent from fore wing; space between Psm and Psc narrow (Fig. 34.8c) APOCHRYSINAE
- At least one of basal subcostal cross-vein and intramedian cell, usually both, present in fore wing; space between Psm and Psc not conspicuously narrow (Fig. 34.1) 2
- 2(1). Fore wing lacking jugal lobe; Psm merges with outer gradate vein series; no more than 2 gradate series in Australian species CHRYSOPINAE
- Fore wing with jugal lobe; Psm merges with inner gradate series, Psc merges with outer gradate series; 3 or more gradate series in Australian species NOTHOCHRYSINAE

The primitive NOTHOCHRYSINAE are represented by 2 endemic genera in the south-east, *Dictyochrysa* (3 spp.) and *Triplochrysa* (2 spp.). These have 2 tibial spurs and relatively complex venation (Fig. 34.8b), and are rather rare. APOCHRYSINAE, sometimes considered a tribe of Chrysopinae, contains only one Australian species. *Oligochrysa lutea* (Fig. 34.8c) occurs along the east coast and on Norfolk I. It has very long antennae, in common with non-Australian representatives in related genera.

CHRYSOPINAE, by far the most diverse group, are taxonomically confusing and many of the species placed in *Chrysopa* (25 spp.) are likely to be transferred to other genera as this group becomes better understood. Australian Chrysopinae also include single species of 2 endemic genera (*Calochrysa*, *Nothancyla*), and representatives of the predominantly tropical *Ankylopteryx* (4 spp.) and *Glenochrysa* (5 spp.). *Italochrysa* (9 spp.) are robust species with the intramedian cell quadrangular.

Most biological information is limited to Chrysopinae. The eggs are usually long stalked, except in the Hawaiian genus *Anomalochrysa*, and the stalks may be several times the length of the egg. Larvae (Figs 34.11f–h) are active, generalist predators, and those of many species rapidly cover themselves with debris (held in place by long curved hairs) which may include the sucked-out remains of their prey. The pupal cocoon may also incorporate debris. Most species are arboreal, and larval development normally takes several weeks so that many species undergo several generations during the warmer parts of the year. A European species of *Italochrysa* is a specialist predator in nests of *Crematogaster* ants.

Adult Chrysopinae are commonly predators, but others are specialised to feed on honeydew, and harbour symbiotic yeasts in a crop diverticulum, presumably to facilitate digestion.

10. Psychopsidae. Medium to large species, with wings broad and sometimes strikingly patterned (Fig. 34.2a). Fore wing length 12–30 mm. Antennae never more than half length of fore wing, and slightly thickened. Venation with 'vena triplica' (Sc, R and Rs run parallel for a considerable length and are connected by short cross-veins) and generally dense with large numbers of Rs branches. The expanded costal space occurs also in some members of other hemerobioid families.

Adults are cryptic, active mainly at night, and sometimes live for 1–2 months. The eggs (of the few species known) are oval, unbatched and attached to vegetation by the long axis. Larvae (Fig. 34.12b) occur under thick rough bark of eucalypts, and the instars are of long duration. In the few species studied, the life cycle takes 2 years to complete. The empodium is trumpet shaped in all instars, and segments of the antenna and palp are well defined. Pupation occurs in bark crevices, and the cocoon consists of a loose outer envelope and an inner one of fine silk.

The family has been recorded from the Oriental region but is best represented in South Africa and Australia (New 1989a). Most species in the 2 genera (*Psychopsis*, 12 spp.; *Megapsychops*, 1 sp.) found in Australia appear to be rare. The family is most diverse in eastern Qld and N.S.W., with one species (*Psychopsis mimica*, Fig. 34.2a) in Vic. and S.A. and one (*P. maculipennis*) endemic in W.A. The most spectacular species is *Megapsychops illidgei* (southern Qld) in which the wing markings may resemble a snake head when the insect is at rest.

Superfamily MYRMELEONTOIDEA

Medium to large lacewings, sometimes brightly coloured, and with veins Sc and R₁ fused for a considerable length

towards the wing apex. The various families are easily separable by the key characters. Riek (1970, 1976e) regarded the Myrmeleontidae: Stilbopteryginae as a separate family (Stilbopterygidae) which showed features of both Myrmeleontidae and Ascalaphidae. New (1982b) showed that the Australian genera (*Stilbopteryx*, *Aeropteryx*) are Myrmeleontidae and that the South American *Albardia* is really an ascalaphid, so that the 'family' was an amalgam of unrelated taxa. Ascalaphidae almost always have long, strongly clubbed antennae, and all Australian species have the eyes divided by a horizontal furrow. Myrmeleontidae often have the antennae thickened or incipiently clubbed, but they are relatively short. Some Nymphidae resemble Myrmeleontidae, but their antennae are tapered, and others are broad winged and superficially resemble Osmylidae. Nemopteridae have very long hind wings, and an elongate face.

Larvae of Ascalaphidae and Myrmeleontidae have the hind tibia and tarsus fused, and the eyes (stemma) are usually grouped on a raised tubercle. In Nymphidae and Nemopteridae this fusion does not occur, and the stem-

mata are more or less sessile. Many Myrmeleontoidea are characteristic of arid and semi-arid regions.

11. Nymphidae. This geographically restricted family is regarded as the most primitive group of Myrmeleontoidea. Most species are large (fore wing length 17–43 mm) and the 7 genera (New 1981) are divided into 2 groups on wing shape and the presence or absence of tibial spurs. *Myiodactylus* (Fig. 34.8F) and *Osmyllops* represent a possibly more primitive kind of broad-winged nymphid producing single stalked eggs which yield flattened discoidal arboreal larvae (Fig. 34.12F). The putatively more advanced forms are typified by *Nymphes* (Fig. 34.8E), have narrower wings, and generally look like myrmeleontids with thin antennae. *Nymphes myrmeleonides*, the largest and one of the most common species in the family, lays eggs in characteristic U-shaped groups of 30–40 alternating in two directions so that some eggs are directly attached to the substrate by short stalks and others 'bridge' between these (Fig. 34.6). The larvae (Fig. 34.12G) are litter dwellers and become covered with debris entangled in the long, coiled, dorsal, filamentous

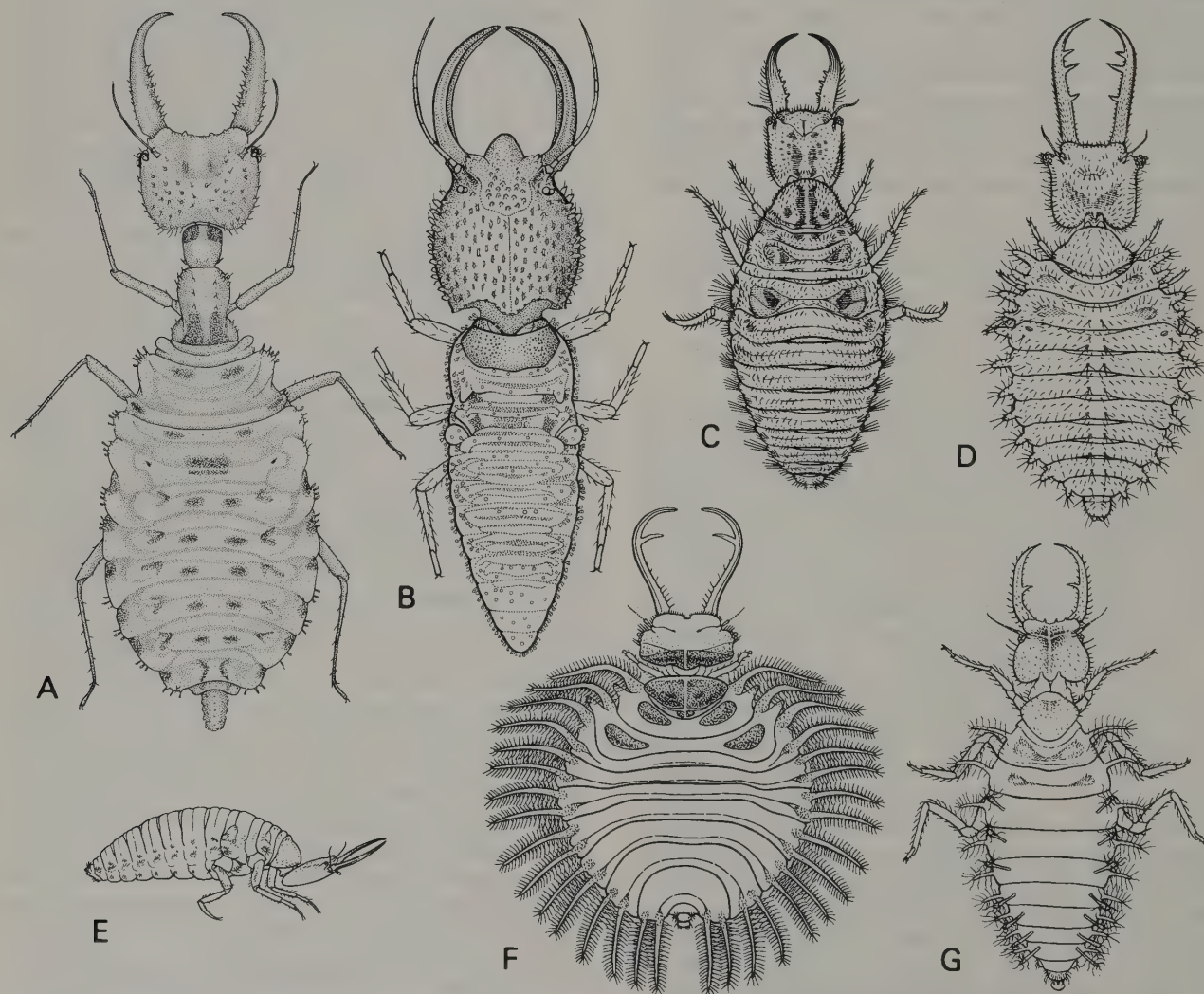


Fig. 34.12 Larvae, dorsal: A, *Austrocroce* sp., Nemopteridae; B, psychopsid; C, myrmeleontid; D, ascalaphid; E, myrmeleontid, lateral; F, nymphid (myiodactylid type); G, nymphid.
[A by M. Mansell; B by A. Hastings; C–E, G by M. Quick; F by R. Ewins]

hairs. All Recent nymphid larvae have a single tooth on the mandible. Fully grown larvae of *Nymphes* are said to pupate in a cocoon in sand or soil. Those of *Osmyllops* do so in cocoons on vegetation or bark. The few species for which data are available seem to be univoltine.

Most species occur in eastern Australia, but there is one western species of *Nymphes* (New 1981, 1986). They are found in open forest habitats and in damp situations. Six species are known from New Guinea.

12. Myrmeleontidae (antlions). By far the dominant family of lacewings in Australia (New 1985a–c), and globally diverse with about 2000 known species. Adults are predominantly medium to large (fore wing 10–72 mm), with long wings (Fig. 34.8H) which are lightly patterned in most species and extensively marked in some. The abdomen is usually long and slender, but is slightly expanded medially in some males, and the folded wings often extend well beyond its apex. Antennae are usually short, occasionally up to half fore wing length, and thickened apically; rarely (*Ceratoleon brevicornis*) very short and subfusiform. Tibial spurs may be present or absent, perhaps reflecting the kind of prey taken. In some American antlions, aphid-feeders lack spurs but congeneric species taking larger prey tend to have large spurs. Claws are simple or with subapical teeth. Adults are usually predatory, although some eat pollen.

Little is known of the biology of most forms. Larvae (Figs 34.12C, E) are ground dwelling or arboreal and it seems that eggs are laid singly, sometimes being scattered in dry soil or sand. Many larvae are subterranean. Some construct conical pits as traps for prey, and lie buried at the bottom with just the open jaws protruding (see pp. 91–92). Other species burrow freely in sand, and move around under the sand or on the surface at night. Still others appear to live on trees, and often closely resemble bark. Larvae often occur under overhangs of rock or under raised logs where they are protected from rain. Some species are univoltine but many have a life cycle substantially exceeding a year, and *Stilbopteryx* in captivity took six years from egg to adult (McFarland 1968).

The dominant antlions in Africa, the brightly coloured, diurnal Palparinae, are absent from Australia.

Key to the Subfamilies of Myrmeleontidae Known in Australia

1. Vein 1A in hind wing with 5 or more branches; antenna very short and strongly clubbed (very large spp.) STILBOPTERYGINAE
- Vein 1A in hind wing with, at most, 2–4 branches; antenna, if short, not as strongly clubbed or species relatively small 2
- 2(1). Femoral sense hair present (as a prominent slender bristle) on hind leg; generally large and densely hairy lacewings, with more than 4 radial cross-veins before origin of Rs in hind wing; fore wing costal cells partially or completely doubled; legs short and stout; claws and tibial spurs strongly arched ACANTHACLISINAE
- Femoral sense hair not present on hind leg; size vari-

ous, usually not densely hairy; 1–6 radial cross-veins before Rs ('presectoral' cross-veins) in hind wing, if more than 2 then fore wing costal cells simple except (rarely) immediately basal to pterostigma; legs usually slender; claws and spurs various MYRMELEONTINAE

The MYRMELEONTINAE is the largest subfamily. Myrmeleontini (3 genera, 23 spp.). *Myrmeleon* (20 spp.) is cosmopolitan and includes the true antlions, with pit-dwelling larvae. Most are slender and dark, although some are yellow. The genus occurs throughout Australia. *Hagenomyia* (1 sp.) is closely related and distinguished by the doubling of fore wing distal costal cells. It is a predominantly tropical genus, with the Australian species limited to northern Qld and closely related to New Guinea forms. *Callistoleon* (2 spp.) are brightly coloured with spotted wings, and occur in the south-east.

Protoplectrini (15 spp.) are generally stouter, often with the fore wing costal cells doubled for much of the wing length. The 6 genera in Australia include *Protoplectron* (8 spp.) containing some of the largest species in the tribe and *Mjobergia* (1 sp.) with brown-spotted wings.

Dendroleontini (83 spp.) are the dominant Australian Myrmeleontidae, *Glenoleon* (31 spp.) being the second largest genus in Australia. Many of the species have a conspicuous dark hind wing blotch (Fig. 34.2B), and a few are common. *Austrogymnocnemia* (18 spp.) are small and relatively narrow winged. *Periclystus* (3 spp.) have falcate wings and are among our most spectacular species. *Froggattisca* (7 spp.) lack tibial spurs (as do *Austrogymnocnemia*) and have the tarsal claws opposable on a dense ventral 'brush' of hairs on the last tarsal segment. In *Mossega* (4 spp.) the hind wing is often larger than the fore wing.

Distoleontini (64 spp.) are also common and widely distributed in Australia, and many of the species are superficially very similar. The large *Distoleon bistrigatus* is one of the commonest species, and occurs also over much of the Pacific. It has a longitudinal dark streak at the apex of the strongly tapered hind wing. *Bandidus* (36 spp.) is the largest myrmeleontid genus in Australia, with many rather small and similar species.

STILBOPTERYGINAE (2 genera, 9 spp.; Riek 1976e) are very large (fore wing length 45–55 mm). *Stilbopteryx* (6 spp.) have the fore wing apex and anterior border darkened; these areas are largely clear in *Aeropteryx*. They are found in arid inland areas and along the north-east coast.

ACANTHACLISINAE (4 genera, 16 spp.) are generally large and densely hairy. Males often have abdominal hair-pencils, thought to diffuse pheromones, and their ectoprocts are elongated ventrally. *Heoclisia* (8 spp.) is widespread and includes the largest Australian myrmeleontid, *H. fulva* with fore wings up to 74 mm long. *H. fundata* occurs in the south-east, including Tas.

13. Ascalaphidae (owl-flies). Medium to large, fore wing length 15–45 mm; differing from Myrmeleontidae on features of the eyes, antennae, venation and genitalia. Most species have the wings hyaline except for the small, well-defined, dark pterostigma, but the apex of the wings

is suffused with brown in the widespread *Suhpalacsa dietrichiae* and a few others (e.g. *Pictacsa*, 3 spp.) have marked wings. Males of several genera have a pronounced dorsal prominence on the anterior of the abdomen (Fig. 34.2D), and *Pilacmonotus* (1 sp.) is densely hairy.

Eggs are laid in clusters of about 30–60 on (and often encircling) twigs or grass stems; 1st instar larvae aggregate there without feeding for some time before dispersing to live singly in litter or on trees. Larvae (Fig. 34.12D) are then predators.

Many of the 15 Australian genera (New 1984a) are closely related and all belong to the ascalaphine tribe Suhpalacsini which is widespread also in Africa and elsewhere. Most Australian species seem to be endemic, and are found predominantly in drier areas. A few species are widespread. Males of *Suhpalacsa* (15 spp.) lack an abdominal prominence.

14. Nemopteridae (thread-wings, spoon-winged lacewings). Fore wing length 12–18 mm. A small family, characterised by the greatly elongate hind wings (Fig. 34.8G) and the rostrate head. The venation is relatively open. In some African and European species the wings

are marked heavily with yellow or brown. Adults sometimes feed from flowers, and larvae are predators. Larvae tend to be found in dust or sand on the floors of small caves or under rock overhangs.

Key to the Subfamilies of Nemopteridae

- Hind wing filiform, not expanded; larvae often with neck elongate and strongly constricted between head and mesothorax CROCINAE
- Hind wing with preapical or apical expansion; larva with neck not markedly elongate or constricted NEMOPTERINAE

CROCINAE are small and delicate species. *Austrocroce* (4 spp.) and *Carnarviana* (2 spp.) occur in drier parts of the continent (Mansell 1983). NEMOPTERINAE include the endemic *Chasmoptera* (3 spp.) (L. E. Koch 1967), mainly from W.A. Larvae of both subfamilies lack any major tooth on the mandible, but known Australian crocine larvae (Fig. 34.12A) have a series of papillae on the inner and outer edges of the mandible.

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